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AILSA M. CLARK

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BY

AILSA M. CLARK

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NOTES ON THE FAMILY AMPHIURIDAE (OPHIUROIDEA)

By AILSA M. CLARK

THIS paper deals primarily with the family Amphiuridae in Mortensen's sense, that is excluding *Ophiactis* and its allies, although it was necessary to include *Amphiactis*, mainly because of a nomenclatorial problem. The relationship between the Amphiuridae and the Amphilepididae is reviewed with the result that the Amphilepididae is reduced to the rank of a subfamily. The taxonomic weight of various characters which have been used in grouping the species of amphiurids is assessed and a modified formula for expressing oral armament concisely is introduced.

My thanks are extended to the International Federation of University Women for a grant which enabled me to study important collections of amphiurids in the United States, providing much of the background to the present work.

The family Amphiuridae now consists of over four hundred nominal species of ophiuroids, most of them living on or burrowing in more or less muddy sand or gravel and some of them very delicate, easily losing the disc, so that a few species are known only from incomplete specimens. The family has recently (1962) been the subject of a revision by Fell, who has divided the larger genera *Amphiura*, *Amphiodia*, *Amphipholis* and *Amphioplus* into groups of more manageable size which are unfortunately rather artificial in my opinion.

The family was established in 1867 by Ljungman, though with the now extraneous subfamilies Ophiacanthinae and Ophionereidinae included (since raised to family rank), while his subfamily Amphiurinae comprised five divisions, of which the present Ophiactidae made two (*Hemipholis* being separated from *Ophiactis* and *Ophiopholis*), *Amphilepis* a third and the amphiurids proper the other two : *Amphipholis*, *Ophiophragmus* and *Ophiostigma* in one and *Ophiocnida*, *Amphiura*, *Ophiopeltis* and *Ophiocentrus* in the other.

Lyman (1882) in his " Challenger " report merged *Amphipholis* and *Ophiopeltis* with *Amphiura* but recognized *Ophiocnida*, *Ophiophragmus*, *Ophiostigma* and *Ophiocentrus*, as well as *Ophionema* and *Ophionephthys*, the last two having been set up by Lütken (1869).

In 1899 Verrill subdivided *Amphiura* on the basis of differences in the number and arrangement of the oral papillae, reviving *Amphipholis* Ljungman and establishing two new genera, *Amphiodia* with three (rarely four) oral papillae on each side of each jaw, all of them arising from the dental and oral plates, with no papilla on the adoral shield and *Amphioplus* with four or five oral papillae, the outermost one at least arising from the adoral shield.

Although he recognized the distalmost oral papilla (sometimes also the third one) as representing the scale or scales of the distal or second oral tentacle, Verrill makes no special mention in his keys to the occurrence of the *first* oral tentacle scale in his two new genera. When present, this scale arises at a higher level in the mouth slit above the oral papillae.[1]

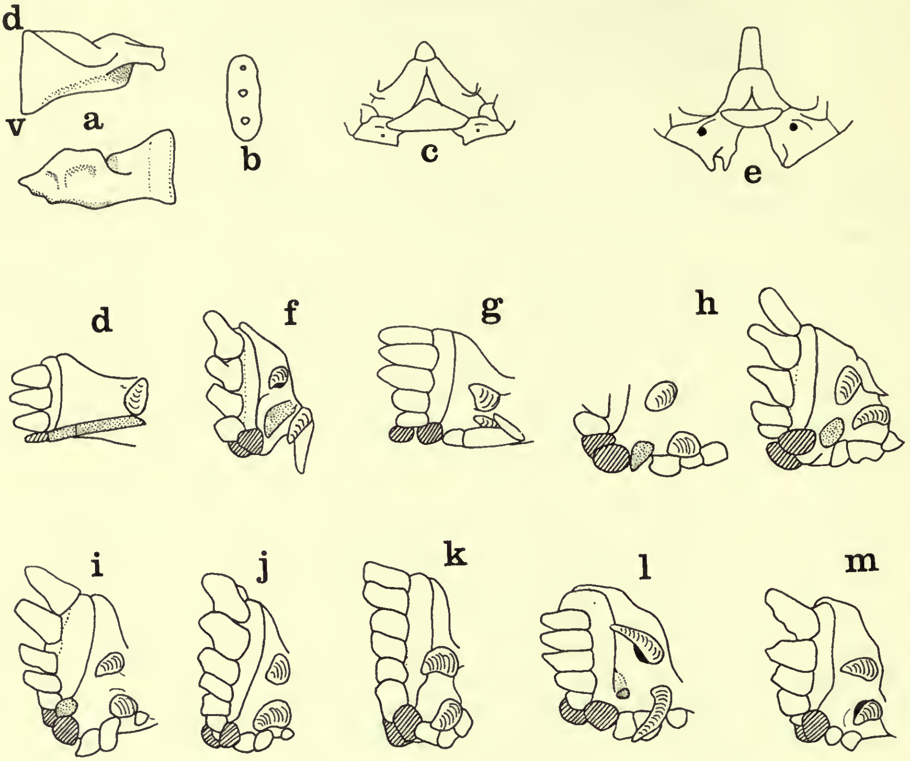

Fig.1, a–d. *Amphilepis norvegica* (Ljungman), B.M. reg. no. 98.5.3.688, Trondhjem Fjord, Norway ; a. Oral plate in adradial view (above) and abradial view (below), b. dental plate, c. dorsal (internal) view of a whole jaw and d. adradial view of projecting part of intact jaw (compare with usual ventral view, fig. 8f). e. *Amphiura chiajei* Forbes, 98.5.3.700, same locality, dorsal view of jaw for comparison with c. f–m. Adradial views of projecting part of intact jaws of : f. *Amphiura filiformis* (O. F. Müller), 72.2.3.156, Vigo Bay, Ireland ; g. *Amphipholis squamata* (Delle Chiaje), 1937.12.31.1, Beachy Head, Sussex ; h. *Amphioplus abditus* (Verrill), 90.8.23.43, Martha's Vineyard, two jaws of same specimen (see fig. 9f for ventral view) ; i. *A. archeri* A.M.C., 1956.5.23.1, paratype, Ghana, two jaws of same specimen, the left-hand one with the only oral tentacle scale ; k. *A. depressus* (Ljungman), 82.12.23.375, Fiji ; l. *A. integer* (Ljungman), Morrumbene Estuary, Mozambique ; m. *Amphiodia occidentalis* (Lyman), 98.11.28.10, Queen Charlotte Is., B.C. [The oral tentacle scale(s), where present, is stippled and the infradental papillae cross-hatched.]

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[1] This scale or papilla has been given a variety of names by ophiuroid specialists and even by the same person at different times. The following people have called it the " first oral tentacle scale (or papilla) " : Lyman, Verrill, Koehler in 1905, H. L. Clark, Mortensen and Thomas. Others, including Matsumoto,

Subsequently other specialists, including Matsumoto (1915 and 1917), Djakonov (1954) and Fell (1960) in their keys to the genera of Amphiurids, have included the presence of the first oral tentacle scale as characteristic of *Amphioplus* as opposed to its absence in *Amphiodia*. In fact a number of species which do not comply with this requirement have been referred to these genera, particularly as regards *Amphioplus*, which is subdivided accordingly further on in this paper.

After Verrill's the next important contribution to the study of the family was that of Matsumoto (1917) who devised a formula to express the occurrence of the oral papillae on each side of a jaw. In his scheme the roman number " I " represents the infradental papilla (the pairing of which at each apex is characteristic of the family), " II " is the superficial papilla or papillae on the side of the oral plate and " III " the papilla or papillae on the adoral shield. By this formula the oral papillae of *Amphioplus* are +I+II+III and those of *Amphiodia* +I+II−III. However, Matsumoto made the proviso that " when a papilla arises partly from the oral plate and partly from the adoral shield it is referred to the second group " (i.e. II). Since such a dual origin is shown by many of the species of *Amphiura*, particularly those with the distal papilla spiniform unlike that of *A. chiajei* the type-species, then Matsumoto's designation of *Amphiura* as +I−II+III is not always correct, although it does express the discontinuity of the series of oral papillae so characteristic of the genus. It seems to me that the proviso should be ignored and group III expanded to include species with the distal papilla arising from the distal end of the oral plate. However, a more elaborate formula is really needed to help pinpoint the position and occurrence of the individual oral papillae more precisely, as well as to cover the oral tentacle scale. Unfortunately Matsumoto's formula does not lend itself to subdivision and qualification. Accordingly I put forward the following alternative devised by Dr. J. P. Harding, Keeper of Zoology. The examples given after each paragraph show the evolution of the formula stage by stage.

1. The individual papillae are represented by the letter m, so that most *Amphiura* species can be expressed as mm and *Amphioplus* as mmmm (see figs. 2, 3 and 9).

2. The three main areas involved, corresponding to Matsumoto's I, II and III, namely the apex of the jaw below the dental plate, the side of the oral plate and the edge of the adoral shield, are delimited from each other by two commas, thus most species of *Amphiura* become m,,m and *Amphioplus* can be m,mm,m.

3. When a papilla arises jointly from two adjacent loci, for instance at the junction of oral plate and adoral shield, then the m is split up into two ns with the comma between and for emphasis a linking bar above, thus $\mathrm{m},\overparen{\mathrm{n},\mathrm{n}}$ for certain species of *Amphiura* which cannot be shown as m,,m and $\mathrm{m},\mathrm{m}\overparen{\mathrm{n},\mathrm{n}}\mathrm{m}$ for most species of *Amphioplus*. (There are also a few species of *Amphioplus* in which the fourth and

Djakonov, Chang and Fell, have used " internal ", " lateral ", " additional " or " supplementary papilla ", while Koehler in 1914 used " intermediate " but in 1922 (possibly altered in translation?) called it the " second " papilla. I propose to use the term " oral tentacle scale " even though it is normally more papilliform than squamiform. It seems unnecessary to specify that it is the first such scale since the one or two corresponding scales of the second oral tentacle on the edge of the adoral shield and/or at its junction with the oral plate are universally regarded as oral papillae. However, it should be pointed out that in a few species of *Amphioplus* it becomes more or less superficial in position, in some individuals fitting in to the series of oral papillae so as to become almost indistinguishable from them in ventral view.

distalmost oral papilla is partly based on the first ventral arm plate ; for these it is necessary to add a third comma and to split the last m as well, thus m,m$\overparen{\mathrm{n,n}}\overparen{\mathrm{n,n}}$ but the great majority of species can be dealt with without this refinement.)

4. If there is a significant gap in the series of papillae this is indicated by the insertion of an o, so that for *Amphiura* the formula becomes m,o,mo (or m,o$\overparen{\mathrm{n,n}}$o).

5. The presence or absence of the oral tentacle scale can be shown by + or —t, which can be added at the end of the formula, thus for *Amphioplus* it is usually m,m$\overparen{\mathrm{n,n}}$m +t and for *Amphiodia* m,mm,o —t. Since the oral tentacle scale is rarely in sequence with the oral papillae but normally arises at a higher level it seems better to separate it from the main formula in this way. However, there are a few species, notably of *Amphioplus*, and the type-species of *Ophionephthys*, in which some individuals have a more or less superficial second papilla lateral to the infradental and clearly homologous with the oral tentacle scale, since on some jaws it is set at a higher level. This is indicated by equating t with the first m in group II, which can be linked within brackets ; thus in *Amphioplus abditus* (figs. 1 h and 9 f–i) the formula may be m,(m = t)m,o$\overparen{\mathrm{n,n}}$ for some series but m,om,o$\overparen{\mathrm{n,n}}$ +t or m,mm,o$\overparen{\mathrm{n,n}}$ +t for others.

6. Finally, if one papilla is enlarged, this can be shown by the use of capital letters, thus m,o,M +t for *Amphiura chiajei* or *mediterranea* or m,m$\overparen{\mathrm{N,N}}$m + or —t for *Amphioplus hastatus* (see figs. 2j and 9p,q).

As a parallel to this formula, it may be of use in discussing the genera of Amphiurids if the four main arrangements of oral papillae, those of *Amphiura*, *Amphiodia*, *Amphipholis* and *Amphioplus*, are designated as A to D respectively, as follows:

A *Amphiura* (usual formula m,o,mo +t)
B *Amphiodia* (usual formula m,m$\overparen{\mathrm{n,n}}$ —t)
C *Amphipholis* (usual formula m,m$\overparen{\mathrm{N,N}}$ —t)
D *Amphioplus* (usual formula m,m$\overparen{\mathrm{n,n}}$m +t)

Most of the genera of the family can then be simply qualified by one letter or the other, for instance *Amphiacantha* (D), having *Amphioplus*-type oral armament, although a few such as *Ophionephthys* cannot be fitted into any one category.

Although this particular sequence of genera with two, three and four oral papillae is the logical one to adopt, it must be emphasized that *Amphiura* and *Amphioplus* are probably more closely related to each other than either is to *Amphiodia* or *Amphipholis*. This is discussed further under the heading of *Amphioplus*.

Until 1962 the most important characters used for separating many amphiurid genera were those furnished by modifications of the disc. For instance *Ophiocentrus* (A), *Ophiocnida* (B), *Ophiostigma* (C) and *Amphiacantha* (D) have spinelets on some of the disc scales, while *Acrocnida* (A), *Amphichondrius* (C) and *Paracrocnida* (D) have the ventral disc scales either thickened and themselves almost granuliform (*Acrocnida* and *Paracrocnida*) or else covered with superficial granules (*Amphichondrius*). However, Thomas (1962) has cast some doubt on the taxonomic value of some disc modifications, notably the development of the marginal " fence " of papillae in *Ophiophragmus* (B), since he has observed some West Indian individuals in which this is completely lacking, so that they are superficially indistinguishable from *Amphiodia.* Since the West Indian species concerned are very liable to lose and regenerate their discs, like a number of other Amphiurids, I think it important that a proper study be made of the resultant disc modifications. Almost certainly the primary rosette with enlarged central and five radial plates is lost in regeneration and the proportions of the radial shields may be altered, though possibly the latter is only transitory; just how much any armament is affected remains to be seen.

In his revision of the four largest genera of the family, Fell (1962a) attempted to subdivide them firstly on the basis of another character provided by the disc—namely the extent of the disc scaling, which in some species is reduced so that the skin is naked, semitransparent and appears dark in preserved specimens—and secondly by the number of tentacle scales.

More or less extensive lack of scaling on the disc is not an entirely new character for distinguishing genera in this family, extreme reduction of the scaling having been used as the main distinction of *Ophionema* and *Ophionephthys* by Lütken (1869) as well as of *Ophiopeltis* Düben and Koren (1845), though the last-named was for eighty years regarded as a synonym of *Amphiura* until revived by Fell.

It seems to me best to consider first the use of these two characters as they bear on the subdivision of *Amphiura* and then to go on to deal with the other nominal genera in the light of this study.

AMPHIURA Forbes

Amphiura Forbes, 1843 : 149–150 ; Lütken, 1859a : 54–55 ; Ljungman, 1867 : 318 ; Lyman, 1882 : 122–126 ; Verrill, 1899a : 24, 25–26 ; 1899b : 306–308 ; Matsumoto, 1917 : 194 ; Fell, 1962a : 4–5, 11–12 ; 1962b : 81. Type-species : *A. chiajei* Forbes, 1843, designated by Verrill, 1899, Lyman's earlier (1865) designation of *A. filiformis* (O. F. Müller) being invalid, this not being among the three species included by Forbes, namely *Amphiura florifera* Forbes (a synonym of *A. chiajei* according to Lütken (1869 : 75) followed by Ljungman), *A. neglecta* (a synonym of *Amphipholis squamata* according to Lütken) and *A. chiajei* itself.

Fell's subdivision of *Amphiura* on the basis of the extent of disc scaling and the number of tentacle scales can be represented in a grid as shown below.

		Tentacle scales		
		0	1	2
Disc	fully scaled	*Nullamphiura*	*Monamphiura*	*Amphiura*
	partly scaled	*Icalia*	*Pandelia*	*Hemilepis*
	more than half naked	*Ophiopeltis*[1]	*Amphinephthys*	

Apart from *Amphiura* itself, all these names were new except for *Ophiopeltis* and *Hemilepis*. *Ophiopeltis* was described with the rank of a genus by Düben and Koren (1845) but *Hemilepis* was a name first used by Ljungman (1871) together with *Ophiopeltis* (spelled *Ophiopelte*) for two groups of Atlantic species of *Amphiura* with partial or almost complete lack of disc scaling respectively ; these names might

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[1] *Ophionema* Lütken was not taken into consideration by Fell but falls into the same section of the grid as *Ophiopeltis*.

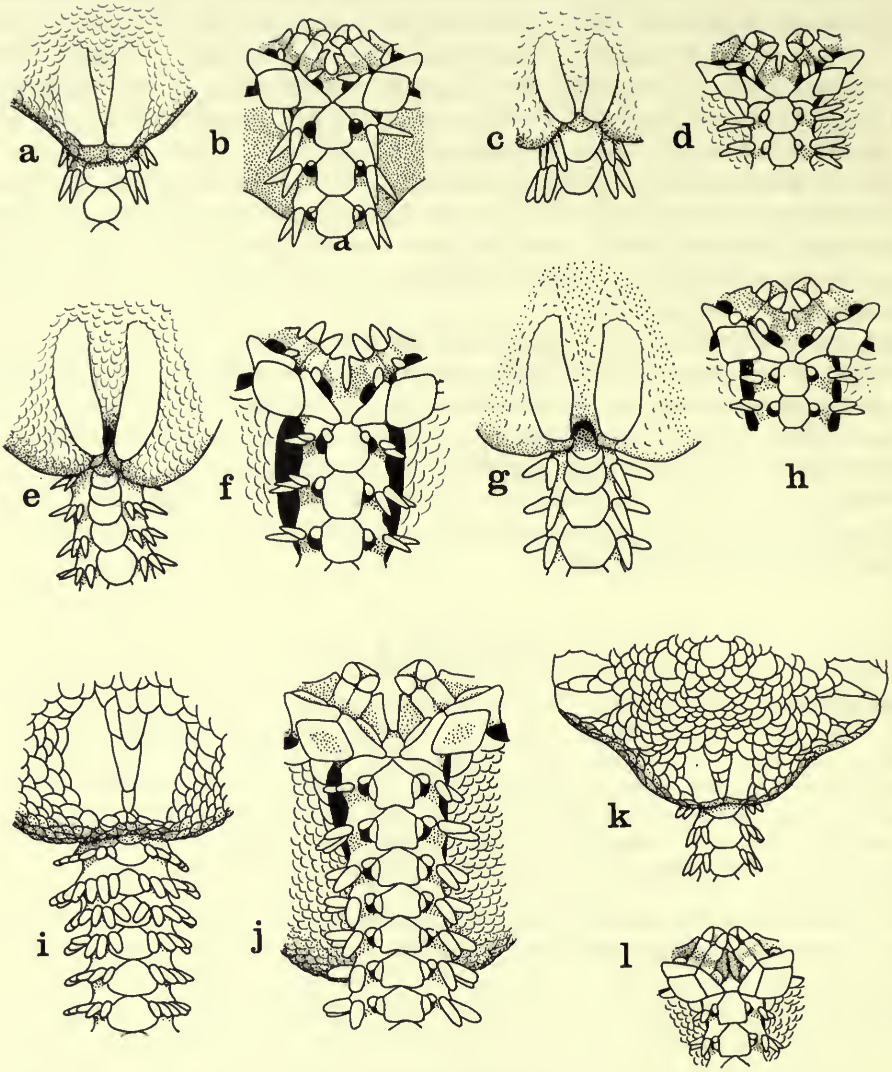

FIG. 2. Dorsal and ventral views of parts of *Amphiura* spp. a and b. *A. semiermis* Lyman, M.C.Z. no. 1343, " Blake " st. 44, West Indies ; c and d. *A. brachyactis* H.L.C., M.C.Z. 4933, holotype, Broome, NW Australia ; e and f. *A. abbreviata* Koehler, Copenhagen Museum collection, Amboina ; g and h. *A. microsoma* H.L.C., M.C.Z. 3736, holotype, Torres Strait area (there are exceedingly tenuous disc scales in the stippled area, which are impossible to outline without over-emphasizing their distinctness, as well as those shown around the radial shields) ; i and j. *A. mediterranea* Lyman, M.C.Z. 1330, syntype, Nice, S. France ; k and l. *A. stepanovi* Djakonov, M.C.Z. 1346 (labelled as syntype of *A. stepanovii* Tscherniawsky, a nom. nud ; d.d. only 3 mm.), Sevastopol, Black Sea. [In e and g the separation of the radial shields is probably unnatural and due to shrinkage in preservation.]

therefore be interpreted as of subgeneric rank as used by Ljungman. Lyman (1882) ignored them when dealing with *Amphiura* in his " Challenger " report but Verrill (1899 a and b) included both names to cover small *groups* of species of *Amphiura* (again without precisely designating them as subgenera) ; also Koehler (1914) mentioned *Hemilepis* only as a " group " name, while Matsumoto (1917) inferred that it is synonymous with *Amphiura*, together with *Ophiopeltis* and *Ophionephthys*.

Because of the great number of species of *Amphiura*, the usual practise when describing new ones has been to restrict comparisons to other species with the same combination of tentacle scale number and disc covering, some specialists having gone so far as to call these similarly-endowed species a " group ". In keys also these two characters have been used for convenience to split up the large number of species involved. However, from the time of Lyman's " Challenger " monograph (1882) until Fell's paper of 1962, no-one has regarded the groups so formed as sufficiently distinct to warrant even a subgeneric distinction.

The taxa of Fell's with reduced disc scaling may be considered first.

Of the four species included in **Hemilepis** by Ljungman, Fell designated **Amphiura semiermis** Lyman, 1869 (fig. 2a, b) as type-species and referred twenty other species to the genus. *A. semiermis* has rather indistinct scales on the dorsal side of the disc and although in some specimens these cover the whole dorsal side stopping at the margin, in others they are lacking interradially and reduced centrally too. Koehler's photograph (1914, pl. iv, fig. 6) shows that the holotype of **Amphiura latispina** Ljungman, 1867b (*Hemilepis* according to Fell) also has the dorsal scaling reduced, the interradii being bare (but for a few isolated scales) and the central scales also inconspicuous so that the scaling appears to be limited to the five radial areas around the pairs of radial shields. This condition of the disc scaling is at variance with Fell's diagnosis of *Hemilepis* as having the disc " scaled above but wholly or partly naked below " but approaches his *Amphinephthys* in which the disc is " naked above and below save for the radial shields and a narrow zone of scales bordering the shields ".

Amphinephthys itself is inconsistent among Fell's other nominal genera, as he himself admits, since it spans two spaces in the grid, including species such as the type, *Amphiura crossota* Murakami, 1943, with two tentacle scales and also *A. microsoma* H. L. Clark, 1915 (fig. 2g, h) with only one scale. *Amphinephthys* is otherwise distinguished by having the disc covered with skin except for scales around the radial shields. I have not seen any material of *A. crossota* but have been able to examine the holotype of **Amphiura microsoma**, which does have scales in the skin of the disc, though these are so fine and nearly transparent that when dried the skin turns dark and appears to lack calcification. Also H. L. Clark (1938) has referred small specimens with fully-scaled disc to the species. The type specimen of the closely related (if not conspecific) nominal species *Amphiura brachyactis* H. L. Clark, 1938 (also from Australia) (fig. 2c, d) has slightly more opaque disc scales, though they are still obscured in the skin. **Amphiura diacritica** H. L. Clark, 1938, which has two tentacle scales like *A. crossota*, was also referred to *Amphinephthys* by Fell, although the type specimen was described as having obscured scales in the ventral skin of the disc, though not in the dorsal side.

Another species which Fell referred to *Amphinephthys* (though doubtfully) was **Amphiura polyacantha** Lütken and Mortensen, 1899, from the East Pacific off Panama, his doubt being aroused by the reversal of the names *polyacantha* and *gymnogastra* on the caption to Lütken and Mortensen's plate ix, though the correct figures 3–5 are quoted both in their text and on the plate itself. These figures show that *A. polyacantha* does have the scale reduction characteristic of *Amphinephthys* and also that it is very similar to the type specimen of **Amphiura arcystata** H. L. Clark, 1911 from California, though in that the disc scaling is even more limited in extent. As I noted in 1965, *A. arcystata* was referred not to *Amphinephthys* but to *Hemilepis* by Fell, apparently as a compromise measure between the three specimens figured by H. L. Clark, only one of which could be described as having the disc scaled above only, a condition supposed to be diagnostic of *Hemilepis*. One of the other specimens figured by H. L. Clark (1911, fig. 58d–f, p. 146) has the scales around the radial shields more extensive on the dorsal side than those of the type but still not quite continuous interradially or centrally and not extending on to the ventral side at all, while the other (fig. 58g–i) has scales all over both sides of the disc, relatively shorter radial shields and fewer and sharper arm spines (judging from the figure). It might seem hard to believe that these two specimens are conspecific with the type or possibly even with each other) since their proximal dorsal arm plates are quite a different shape, markedly rhombic and only narrowly contiguous as opposed to rounded with only the slightest lateral angles in the type. However, the Japanese specimens which I studied in 1965 do have more nearly ovate plates. Matsumoto (1917) recorded some additional Japanese specimens as *arcystata*, noting that the larger ones have discs of the " *Ophionephthys*-type " (i.e. with scales only around the radial shields) ; presumably the smaller ones have more extensive scaling. Djakonov (1954) also found that some small specimens from the north-west Pacific have fine granuliform scaling on both sides of the disc in contrast to the usual condition.

Further records of *A. arcystata* from the eastern Pacific have been made by May (1924), Nielsen (1932) and Ziesenhenne (1937). May noted that specimens from Monterey Bay usually have the disc naked at the centre and interradially but sometimes the upper side is completely scaled. Nielsen found that all his nine specimens from La Jolla had the discs naked except around the radial shields and the same was probably true of Ziesenhenne's seven lower Californian ones since he noted that on the dried specimens the discs were brown but the radial shields white. The only specimens of *A. arcystata* in the British Museum collections, for which I am indebted to Captain Ziesenhenne, are three from Santa Cruz Island, southern California, all of which have the discs mainly covered with dark brown skin in which there is not a trace of imbedded scales. The shape of the dorsal arm plates in all of them is rounded, not at all rhombic.

It remains to be seen from direct comparison of abundant material from both sides of the North Pacific whether Japanese specimens can be distinguished in any way from Californian ones. The extent of the disc scaling does not appear sufficiently constant to warrant a specific distinction (let alone a generic one). A comparison between *Amphiura arcystata* and the type-species of *Amphinephthys*, *Amphiura crossota* Murakami, from the Caroline Islands is also called for.

Yet another name which should be considered in dealing with *Amphiura arcystata, polyacantha* and *gastracantha* is **Amphiura verticillata** Ljungman, 1867, known only from a damaged specimen from the Galapagos Islands. This was described by Ljungman as having minute scales covering the disc and accordingly Fell retained it in *Amphiura* but Koehler's photographs (1927a, pl. ii) show scales apparently only remaining in oval areas around the radial shields, as if the interradial and central scales were much less substantial and so were easily lost or obscured. The distal oral papilla of *A. verticillata* arises from the oral plate as in the Californian type of *arcystata,* not from the edge of the adoral shield as in H. L. Clark's figures of the other (Japanese) specimens which he named *arcystata.* The shapes of the radial shields, oral and adoral shields and of the ventral arm plates in *verticillata* are not unlike those of the type of *arcystata* and of *polyacantha* but the almost rectangular dorsal arm plates, thick distal oral papilla and somewhat square-tipped arm spines of *verticillata* may provide significant differences.

Thus we have three closely related species, *Amphiura arcystata, polyacantha* and *verticillata* referred to three different nominal genera, *Hemilepis, Amphinephthys* and *Amphiura,* by Fell's system.

There are several examples of differences in the extent of the disc scaling in individuals which have been attributed to separate species as well as others such as those of *arcystata* already cited which are considered conspecific. For instance, H. L. Clark (1938) described **Amphiura brachyactis**, which Fell placed in **Pandelia** on account of its single tentacle scale and the occurrence of fine scales (by implication in the description) on the upper side of the disc only. Clark commented that *brachyactis* is very closely related to *A. microsoma* (see above p. 9) which he had described in 1915 and which Fell refers to *Amphinephthys* since the type was described as having the disc almost naked above as well as below. However, in 1938 H. L. Clark also recorded some specimens which he attributed to *microsoma* even though their discs were distinctly covered with scales on both sides. I have examined the holotypes of both nominal species and find that even in *microsoma* there is an almost continuous coat of scales although these are so fine and transparent as to be almost obscured by the skin, which appears more or less dark in colour except around the radial shields where the scaling is more nearly opaque. The two species appear to be distinguished by the relative arm length but they are certainly congeneric. Among the species with no tentacle scales, **Amphiura syntaracha** H. L. Clark, 1915, which Fell refers to **Icalia**, has the disc scaled except in the proximal parts of the ventral interradii but is otherwise very similar to four other Japanese nominal species with much more reduced scaling, namely *A. ecnomiotata* H. L. Clark, 1911, *aestuarii* Matsumoto, 1915, *vadicola* Matsumoto, 1915 and *sinicola* Matsumoto, 1941, all of which Fell places in *Ophiopeltis.* Further, Djakonov (1954) has described two forms, *incompleta* and *profundi* of **Amphiura psilopora** H. L. Clark, 1911 (lacking tentacle scales so that Fell refers it to **Nullamphiura**), these forms being distinguished from the fully-scaled form *psilopora* by having the disc skin-covered ventrally with either coarse or fine soft skin. Mortensen (1936) has noted specimens of **Amphiura deficiens** Koehler, 1922b (*Icalia* according to Fell) in which the disc is almost completely scaled ventrally, unlike the condition in the type-material.

Another species of Djakonov's, **Amphiura inepta** (1954) is referred by Fell to **Monamphiura** (with one tentacle scale and the disc fully-scaled), presumably on the basis of Djakonov's figures. However, the description notes that the disc appears bare ventrally in specimens preserved in spirit although dried specimens show very small, thin, rounded scales arranged loosely in the ventral interradii.

Until much more work has been done on individual and seasonal variation in the disc scaling of these burrowing amphiurids it is difficult to decide to what extent it can be used in taxonomic distinctions, even at specific level, unless supported by other characters.

With regard to the use of the number of tentacle scales as a generic character, there are several species of *Amphiura* which have been shown to be variable in this respect. An extreme example is *Amphiura belgicae* Koehler, 1900, which Mortensen (1936) notes may have the tentacle scales numbering two, one or none, some specimens having one number throughout while in others it varies even on different pores of the same arm. Other species may also have mixed scale counts, the proximal or at least the basal pores having a different number to the distal ones, or odd numbers may occur at random, one number may predominate in certain individuals or immature specimens may have fewer scales than adults of the same species. Examples of all these conditions include *Amphiura angularis* Lyman, 1879, *anomala* Lyman, 1875, *aster* Farquhar, 1901, *concolor* Lyman, 1879, *dacunhae* Mortensen, 1936, *fibulata* Koehler, 1913, *rosea* Farquhar, 1893, *simonsi* A. M. Clark, 1952, *stimpsoni* Lütken, 1859, *sundevalli* (Müller & Troschel, 1842) and *verticillata* Ljungman, 1867. Accordingly I very much doubt the wisdom of giving generic weight to the number of tentacle scales in this family.

As a result of these observations, I consider that the following should be referred to the synonymy of *Amphiura* Forbes, 1843 :

Ophiopeltis Düben & Koren, 1845 (type-species *O. securigera* Düben & Koren, 1845) [but see below].
Hemilepis Ljungman, 1871 (type-species *Amphiura semiermis* Lyman, 1869).
Amphinephthys Fell, 1962 (type-species *Amphiura crossota* Murakami, 1943).
Icalia Fell, 1962 (type-species *Amphiura denticulata* Koehler, 1896, a synonym of *A. fragilis* Verrill, 1885).
Pandelia Fell, 1962 (type-species *Amphiura hinemoae* Mortensen, 1924).
Nullamphiura Fell, 1962 (type-species *Amphiura psilopora* H. L. Clark, 1911).
Monamphiura Fell, 1962 (type-species *Amphiura alba* Mortensen, 1924).

The range of form within the assemblage of species so reunited is extensive and some natural groups distinguished by combinations of characters may prove to be recognizable but I very much doubt whether these should be ranked higher than subgenera.

Of these seven names, there is only one which I think merits recognition as a subgenus of *Amphiura*, this is **Ophiopeltis** as noted by me in 1966 when describing a new Australian species.

Among the many amphiurids with no disc armament and reduced tentacle scales coupled with *Amphiura* (A)-type mouth parts, the most obviously different from the type-species of the genus, *A. chiajei*, are those which have no tentacle scales at all combined with extremely reduced disc scaling. Some of these have been referred in the recent past to the genus *Ophionephthys* but, as Fell has pointed out, are clearly not congeneric with the type-species, *O. limicola* Lütken, 1869, from the West Indies, since that species has two (rarely three) small oral papillae distal to the infradental one, besides an oral tentacle scale, all arising from the *oral* plate (its formula being normally m,omm,o +t), one small tentacle scale on most of the arm pores, a conspicuous row of scales around the periphery of the disc dorsally and the adoral shields meeting widely at their proximal (interradial) ends. In Fell's revision a generic distinction is rightly made between *O. limicola* and these other species, namely *O. ecnomiotata* (H. L. Clark, 1911), *O. africana* Balinsky, 1957, *O. decacantha* H. L. Clark, 1938, *O. heptacantha* Mortensen, 1940 and *O. octacantha* H. L. Clark, 1915, all of which he regards as congeneric with *Ophiopeltis securigera* Düben and Koren. *Ophiopeltis* was a monotypic genus as originally proposed, including only **Ophiopeltis securigera,** characterized by its very long arms, 12–15 times the disc diameter, completely naked disc, absence of tentacle scales and modification of the middle of the three arm spines with an axe-headed tip (fig. 3b, d).

In 1861 Michael Sars redescribed *O. securigera* and noted that drying renders visible some microscopical imbricating scales in the skin covering the disc. No mention of this had been made by Düben and Koren, who described the skin of the disc as so very thin and soft that it often ruptures in preserved specimens over the arm bases, as it has done in the single (dried) specimen from the Shetland Islands in the British Museum collections, which is the only example of *securigera* available to me and which shows no trace of the microscopic scales noticed by Sars.[1]

It was presumably on the strength of this observation by Sars that Lütken (1869) rediagnosed *Ophiopeltis* as having extremely minute scales in the skin of the disc and accordingly separated off a new genus *Ophionema* characterized by complete absence of any such scales. However, as a supporting character he cited the unspecialized arm spines of the type-species, *Ophionema intricata.*

Two years later in 1871, G. O. Sars described a new species of *Ophiopeltis, O. borealis,* but Ljungman treated *Ophiopeltis* (spelled *Ophiopelte*) as a subgenus of *Amphiura* and expanded it to include *filiformis* (O. F. Müller, 1776), *atlantica* Ljungman, 1867 and *sarsi* Ljungman, 1871, as well as *securigera* and *borealis.*

However, Lyman in his " Challenger " report (1882) and subsequent authors until 1962 have considered *Ophiopeltis* as a synonym of *Amphiura,* not even a subgenus, because of the existence of intermediate species like **Amphiura borealis** (G. O. Sars) with shorter arms and partially-scaled discs but other characters approximating to those of *Ophiopeltis securigera.* The wisdom of this is supported by Mortensen's figure of these two species side by side (1927, fig. 122), showing that they are very similar, differing only in the presence of disc scales over most of the dorsal side coupled with inward divergence of the radial shields and by the lesser modification of the second arm spines in *borealis*. Other species are known in which the disc scaling is intermediate in extent between the complete or almost complete absence of scales in *securigera* and the partial covering in *borealis* but the issue has been clouded by the fact that, with the exception of some Japanese species, these others have been referred to *Ophionephthys*, which Matsumoto (1915 and 1917) maintained in *Amphiura*, being unfamiliar with the type-species, *O. limicola*, the mouth parts of which had not then been figured. The Japanese species described by Matsumoto are *Amphiura aestuarii*, *A. vadicola* and, in 1941, *A. sinicola*, which are more or less intermediate, particularly in the rather wider dorsal and ventral arm plates, between other Japanese species such as *A. syntaracha* H. L. Clark, 1915, which has scales all over the disc except on the proximal parts of the ventral side, and *A. ecnomiotata* H. L. Clark, 1911, subsequently referred to *Ophionephthys* by H. L. Clark in 1915 since it has scaling around the radial shields. Following Matsumoto, Koehler (1922a) also considered *Ophionephthys* as a synonym of *Amphiura*. However, Mortensen in 1924 and 1936 had a different conception of the nature of *Ophionephthys* (identical with that adopted by Fell in 1962); he referred to the genus two species (*stewartensis* and *magellanica*) with tentacle scales present and *Amphioplus* (D)-type oral papillae, of which the discs were assumed to be deficient in scaling just because they were missing in the specimens collected. The fallacy in this has been revealed by the recent discovery of Castillo (1968) that intact *magellanica* has a scale-covered disc and is clearly referable to *Amphioplus* ; probably the same will prove to be true of **Ophionephthys stewartensis**, which should be referred to *Amphioplus* meantime. By 1940 Mortensen had changed his mind and was again describing species of *Ophionephthys* (namely *heptacantha* and *iranica*) with *Amphiura* (A)-type oral papillae, as H. L. Clark had been doing since 1915.

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[1] This specimen of *securigera* also shows two interesting anomalies. Firstly it has a small poorly-calcified tentacle scale on most of the arm pores, which is quite distinct in the dried condition (though could well be inconspicuous in spirit ones). Secondly there are *two* distal oral papillae on each side of all the jaws, the inner of the two arising from the outer part of the oral plate so that the formula is m,om,m+ t. (Fell (1962a) has also observed this phenomenon.) On two of the jaws there is a small median apical papilla between the infradental pair, as may also occur in a number of amphiurids, including *Amphiura borealis.*

The species that Fell has referred to *Ophiopeltis* from *Ophionephthys* are *Amphiura aestuarii* Matsumoto, 1915, *Ophionephthys africana* Balinsky, 1957, *O. decacantha* H. L. Clark, 1938, *Amphiura ecnomiotata* H. L. Clark, 1911, *Ophionephthys heptacantha* Mortensen, 1940, *O. iranica* Mortensen, 1940, *O. octacantha* H. L. Clark, 1915 and *Amphiura vadicola* Matsumoto, 1915 (*A. sinicola* Matsumoto, 1941, which clearly belongs to the same group having been overlooked by Fell). In addition there are three other species which Fell has included in *Ophionema* but which, in my opinion, are close to some of these listed above, namely *Ophionephthys phalerata* Lyman, 1874, *O. tenuis* H. L. Clark, 1938 and *Ophionema hexactis* Mortensen, 1940. Both *phalerata* and *hexactis* have the second from lowest of the arm spines strongly spinose at the tip, while *tenuis* has the corresponding spine on the more distal arm segments modified into an axe-headed shape (a feature not mentioned by H. L. Clark in his description but observable on a paratype in the British Museum collections and also noted by Mortensen in 1940 on one sent to him for comparison with *Ophionephthys iranica*, which species he emphasized is closely related to *tenuis*). On the contrary, the two American species of **Ophionema,** *O. intricata* Lütken, 1869 and *O. hexacantha* Nielsen, 1932, have the arm spines relatively unspecialized, tapering in shape and only slightly blunted and rugose at the tips. In addition these two evidently lack even the narrow area of disc scales round the proximal end of each radial shield which is visible in *hexactis*, *iranica* and *tenuis*. In *securigera* also there is little or no scaling here. I have seen no examples of *Ophionema* myself and can rely only on Nielsen's remarks and figures and Lütken's earlier description (in Danish) of *O. intricata.* Fell did not include the genus in the key given in his main revision, nor did he diagnose it, though this was done in his Australian amphiurid paper, with particular reference to *Ophionephthys tenuis* which he was referring to *Ophionema* (while simultaneously placing the related *iranica* in *Ophiopeltis*).

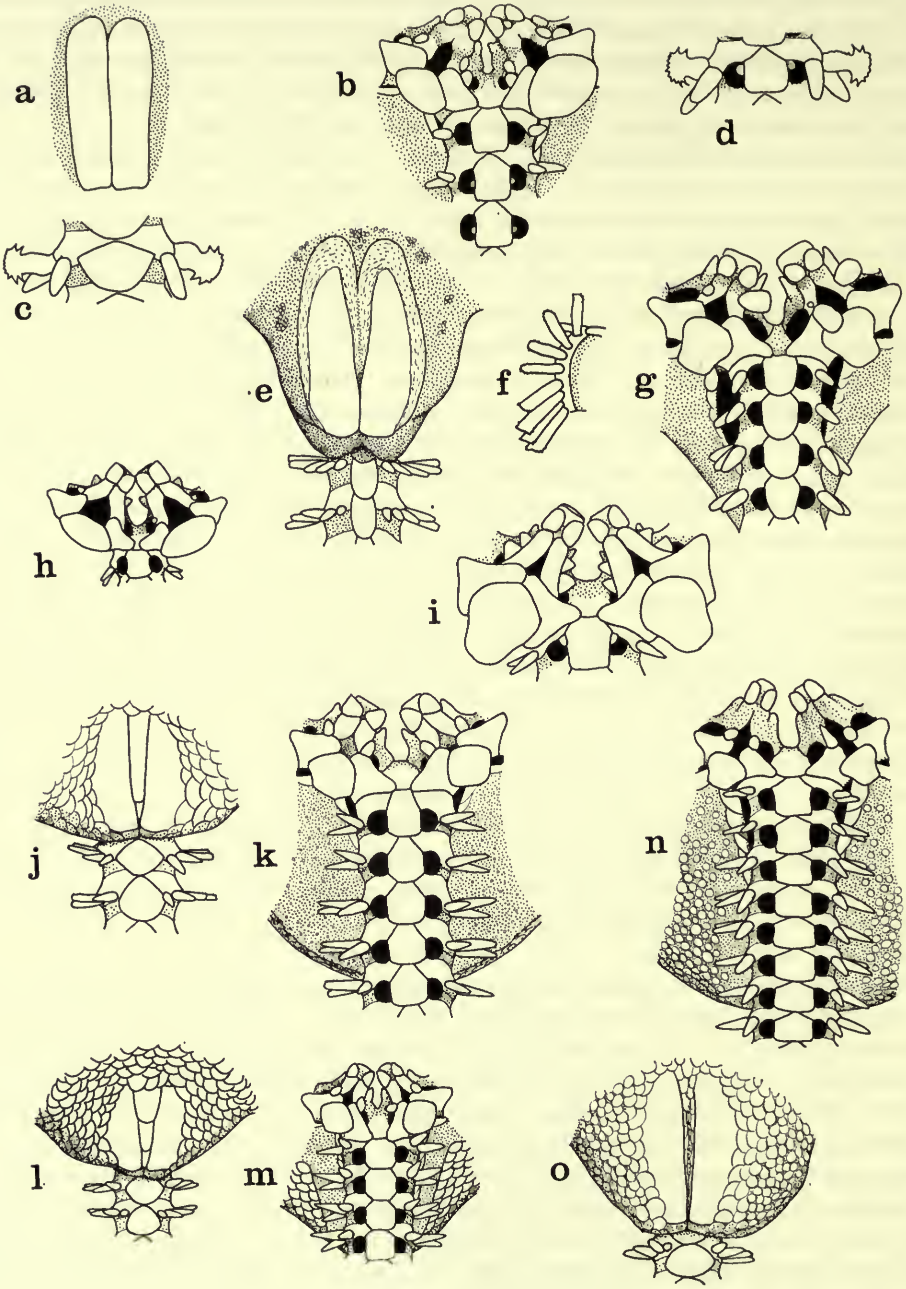
The type-species of *Ophiopeltis, O. securigera,* has only four arm spines proximally and three for most of the length of the arm, of which the middle one is strongly modified into a flattened, axe-headed shape (Fig. 3c, d); the dorsal arm plates are fan-shaped, wider than long and the disc scaling is more or less completely absent so that the bar-like radial shields are parallel. An additional species from southern Australia, *Amphiura* (*Ophiopeltis*) *parviscutata,* was described by me in 1966 and is very closely related to *securigera,* which it resembles in these characters.

The twelve other affiliated species mentioned above fall into two fairly natural groups on the basis of arm structure. In the first come those having not more than five arm spines and only the second from lowest one more or less strongly modified at the tip, with at the same time the arm plates not particularly narrowed so that the dorsal ones are all wider than long. In this group come *aestuarii, iranica, tenuis, phalerata* and *hexactis.* Owing to Lyman's very poor figures of *phalerata* it is difficult to make a proper comparison of it and his statement that its adoral shields are " curved and united at their ends so as to form a continuous ring "—a condition supported by the diagrammatic figure—is completely at variance with the condition found in any of the other species under consideration, all of which have the adorals spaced interradially with a pit between their ends. Only the holotype of *hexactis* is known and this has six arms and three madreporites ; it remains to be seen whether other specimens from the Persian Gulf share this irregularity. The arm spines number four and the second from lowest has a very spinose tip. The four other species all have five arm spines proximally. In this group of five species some have the disc scaling less reduced than others, so that in *aestuarii* and *phalerata* the radial shields are separated proximally on the surface by a wedge of scales, whereas in *iranica, tenuis* and *hexactis* the shields are parallel with scales only at their proximal and abradial ends.

The second group of species, comprising *africana, decacantha, ecnomiotata, heptacantha, octacantha, sinicola* and *vadicola,* is marked by the possession of seven to ten arm spines proximally and several of these, not just the second one, are flattened and markedly square-tipped or spinose at the ends ; also the arm plates are more or less narrowed so that, at least at the base of the arm, the dorsal ones are longer than wide. All these species (with the possible exception of *africana,* the photograph of which does not show the condition clearly) have the radial shields inwardly divergent.

It follows from this that *Ophiopeltis securigera* is more closely related to the first group than to the second and indeed it seems to me that if *Ophionema* is to be maintained as separate from *Ophiopeltis,* then this second group should also be distinguished with the same taxonomic rank.

The question is, what should this rank be? Fell would make it a generic one on a par with his other taxa but I cannot bring myself to do this because the different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groups of species involved are not sharply defined. For instance in European waters *Amphiura borealis* (as already quoted) links *Amphiura* with the type-species of *Ophiopeltis*, while in Japan there is a series of species from *A. syntaracha* H. L. Clark (Fig. 3m, n), still with no tentacle scales but with the disc completely (though loosely) scaled except in the proximal parts of the ventral interradii and with arms at least ten times the disc diameter, through *aestuarii* with more restricted disc scaling but still only five arm spines and relatively wide dorsal arm plates, then to *sinicola*, *vadicola* and finally *ecnomiotata*, with seven to ten spines, progressively narrower arm plates and longer arms. Accordingly I propose to regard these three taxa as subgenera of *Amphiura*. Unfortunately since one of them is split off from *Ophiopeltis* sensu Fell it is necessary to add yet another name to the literature.

AMPHIURA subgenus ***OPHIOPELTIS*** Düben & Koren, 1845, restricted

Ophiopeltis Düben and Koren, 1845 : 437 ; 1846 : 236–238, pl. vi, figs. 3–6 ; M. Sars, 1861 : 14 ; Ljungman, 1867b : 321 ; Lütken, 1869 : 94 (75) ; G. O. Sars, 1871 : 15–17 ; Fell, 1962a : 8–9 ; 1962b : 82. Type-species : *Ophiopeltis securigera* Düben and Koren, 1845.
Amphiura (*Ophiopelte*) : Ljungman, 1871 : 643.
Amphiura (part), Lyman, 1882 and following authors until 1962.

DIAGNOSIS. A subgenus of *Amphiura* in which the disc scaling is absent or reduced to a small area proximal to each of the bar-like parallel radial shields or to a slightly larger patch with a wedge between the proximal ends of the radial shields, which consequently appear divergent ; the arms are extremely long, more than ten times the disc diameter ; the oral shields have only a slight proximal lobe, if any, and the adorals are widely separated interradially (? in *phalerata*) ; the distal oral papilla is never very large and sometimes (*hexactis*) rudimentary ; the dorsal arm plates are wider than long ; the arm spines proximally number four or five, the second from lowest one becoming more or less modified with an axe-headed or very spinose tip, especially on the outer part of the arm, tentacle scales are normally lacking though a poorly-calcified small scale may occur on some pores of certain individuals.

INCLUDED SPECIES. *Ophiopeltis securigera* Düben & Koren, 1845, from northern Europe, *Ophionephthys phalerata* Lyman, 1874, from the Philippines, *O. tenuis* H. L. Clark, 1938, from north-west Australia, *Amphiura* (*Ophiopeltis*) *parviscutata* A. M.

FIG. 3. Dorsal and ventral views of parts of *Amphiura* spp. (except for i). a–d. *A.* (*Ophiopeltis*) *securigera* Düben and Koren, 1953.4.8.138, Shetland ; a. radial shields and a small area of surrounding skin (stippled), b. two jaws (the madreporite on the right) showing the abnormal occurrence of two distal oral papillae each side and incipient single tentacle scales, c. fiftieth arm segment from above and d. from below ; e–g. *A.* (*Fellaria*) *octacantha* (H.L.C.), M.C.Z. 3744, holotype, Torres Strait area (in f the fifteenth free arm segment is shown and the spines are slightly foreshortened ; in g one distal oral papilla is displaced and another, extreme left, lost) ; h. *A.* (*Ophionema*) *intricata* (Lütken) (after Nielsen, 1932) ; i. *Ophionephthys limicola* Lütken (modified from Nielsen and from Thomas, 1962) ; j and k. *A. fragilis* Verrill, U.S.N.M. 32601, holotype, "Albatross" st. 2025, E coast of U.S.A. ; l and m. *A. sarsi* Ljungman, M.C.Z. 1342, syntype, Azores ; n and o. *A. syntaracha* H.L.C., M.C.Z. 1361, holotype, Bay of Yeddo, Japan.

Clark, 1966, from Victoria, Australia, *Ophionephthys iranica* and *Ophionema hexactis* Mortensen, 1940 from the Persian Gulf (the former also taken recently in the vicinity of Karachi, West Pakistan) and *Amphiura aestuarii* Matsumoto, 1915, from Japan. Geographically therefore these are a mixed lot ; *A.* (*Ophiopeltis*) *parviscutata* is the one most closely related to the similarly temperate *A.* (*Ophiopeltis*) *securigera*, while the rest are from the tropical Indo-West Pacific and are morphologically intermediate to some extent with the species of the following subgenus from the same region.

AMPHIURA subgenus *FELLARIA* nov.

Amphiura (part) H. L. Clark, 1911 : 148–149 ; Matsumoto, 1915 : 71 ; 1917 : 211–213 ; 1941 : 339–342.
Ophionephthys (part) H. L. Clark, 1915 : 239–240 ; 1938 : 240–241 ; Mortensen, 1940 : 79–81 ; Balinsky, 1957 : 7–9. [Non *Ophionephthys* Lütken, 1869].
Ophiopeltis (part) Fell, 1962a : 8.

Diagnosis. A subgenus of *Amphiura* in which the disc scaling is reduced to a small area lateral and proximal to each pair of radial shields ; the arms are extremely long, usually fifteen to twenty times the disc diameter but sometimes even longer ; the oral shields have only a slight proximal lobe, if any, and the adorals are widely separated with a pit between their interradial ends ; the distal oral papilla is not rudimentary but may be large and clavate ; the dorsal arm plates are narrow, the basal ones at least, if not all of them, longer than wide ; the arm spines number seven to ten proximally and all or most of them are flattened with their tips rugose and squared-off or slightly flared ; tentacle scales are lacking.

Type-species. *Ophionephthys octacantha* H. L. Clark, 1915, from northern Australia.

Included species. *Ophionephthys africana* Balinsky, 1957, from Mozambique, *Amphiura ecnomiotata* H. L. Clark, 1911, from Japan and *Ophionephthys heptacantha* Mortensen, 1940, from the Persian Gulf ; also *Amphiura vadicola* Matsumoto, 1915 and *A. sinicola* Matsumoto, 1941, from Japan, which are to some extent intermediate with *Amphiura* sensu stricto. **Ophionephthys decacantha** H. L. Clark, 1938, I consider is a synonym of *A.* (*Fellaria*) *octacantha*, having studied the holotypes of both. Despite the name *decacantha*, I could not find more than eight arm spines on any part of the arms of the former and the only apparent morphological difference consists of the barely contiguous proximal dorsal arm plates in the holotype of *decacantha*, those of *octacantha* tending to overlap slightly for most of their width, at least on the proximal segments. D.d. in both is about 5 mm. but the disc of the holotype of *octacantha* is more drastically shrunken and I think that the original size was greater than in the other specimen, which might account for the small difference in arm structure. The type-localities are Friday Island, Torres Strait (*octacantha*) and Broome, north-west Australia (*decacantha*).

It may be noted here that H. L. Clark's figure of the holotype of **Amphiura ecnomiotata** is incorrect in showing the distal oral papillae as long and narrow ; in fact they are very thick and not particularly elongated ; also the oral shields are in reality as wide as long or a little wider. In addition, in the skin of the disc between the radial shields interradially are scattered some very fine scales, not mentioned by Dr. Clark.

AMPHIURA subgenus ***OPHIONEMA*** Lütken, 1869, restricted

Ophionema Lütken, 1869 : 27–28 (9–10), 94 (76), 98 (80) ; Lyman, 1882 : 151–152 ; 1883 : 253 ; H. L. Clark, 1918 : 282–284, pl. 2, figs. 1–3 ; Nielsen, 1932 : 265–267 ; Thomas, 1964 : 159–160. [Non *Ophionema* : Mortensen, 1940 : 79–81 (*O. hexactis*, now referred to *Ophiopeltis*)]. Type-species : *Ophionema intricata* Lütken, 1869.

DIAGNOSIS. A subgenus of *Amphiura* in which the disc scaling is absent and the radial shields are bar-like and parallel ; the arms are extremely long, fifteen to twenty times the disc diameter ; the oral shields have no proximal lobe and the adorals are widely separated interradially ; the distal oral papilla is small and often more or less rudimentary ; the dorsal arm plates are fairly narrow, about as wide as long or a little longer ; the arm spines proximally number five or six and all taper to a rounded and only slightly rugose tip ; tentacle scales are lacking.

INCLUDED SPECIES. *Ophionema intricata* Lütken, 1869, from the West Indies and *O. hexacantha* Nielsen, 1932, from Panama.[1]

It seems advisable at this point to add references and a diagnosis to *Ophionephthys* for comparison with the superficially rather similar subgenera of *Amphiura* just dealt with.

OPHIONEPHTHYS Lütken, 1869

Ophionephthys Lütken, 1869 : 25–27 (7–9), 93 (75), 98 (80) ; H. L. Clark, 1918 (part) : 278–282 ; Nielsen, 1932 : 266, fig. 8 ; Fell, 1962a (part) : 3–4, 15 ; Thomas, 1962 : 680–681. Type-species : *Ophionephthys limicola* Lütken, 1869. [The many references to species other than the type-species apply to *Amphiura* (*Ophiopeltis*), *Amphiura* (*Fellaria*), *Amphioplus* and (in the case of *O? sesquipedalis* Bell) to *Amphiodia* or *Ophiophragmus*.]

DIAGNOSIS. A genus of the family Amphiuridae in which the disc scaling is reduced to a small patch of scales at the proximal end of each pair of radial shields and a line of scales near the edge of the disc extending across the interradii from the distal end of each radial shield ; the arms are extremely long, up to twenty times the disc diameter ; the oral papillae are normally limited to three in each series, the two distal ones on the side of the oral plate as well as the oral tentacle scale (occasionally odd series are found with a fourth papilla but this is nearly always situated also on the oral plate and rarely on the adoral shield) so that the oral formula is normally m,mm,o +t (occasionally m,mmm,o +t and only rarely m,mm,om +t). In the type species the adoral shields meet widely interradially, the oral shields have a large rounded proximal lobe, the dorsal arm plates are as wide as or wider than long and there is a single tentacle scale.

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[1] Since completion of this MS, a paper by Domantay and Domantay (Studies on the classification and distribution of Philippine littoral Ophiuroidea (brittle stars). *Philipp. J. Sci.* **95**: 1–77; 1967) has come to my notice. This includes a description of a new species referred to *Ophionema*, *O. philippinensis* (p. 25), the affinities of which are difficult to assess from the information given. It is clear from the drawing of the upper side (fig. 4) that the disc has been lost, the central structure being the oral frame. The excessively high ratio of arm length to d.d. of 25–30 : 1 (d.d.—in fact the diameter of the oral frame—being given as only 2 mm.) is almost certainly incorrect, the true ratio being probably much lower, rendering unlikely a close relationship with *Ophionema intricata*.

REMARKS. Having started as a monotypic genus, I consider that *Ophionephthys* should revert to that condition. The treatment of some of the nominal species which have been referred to it since 1869 is dealt with in the discussion leading up to the subgenera of *Amphiura* above but an extended account of the history is needed.

The species which have been referred to *Ophionephthys* since 1869 fall into two categories. The first includes those with *Amphiura* (A)-type oral papillae, namely *phalerata* Lyman, *ecnomiotata* (H. L. Clark), *octacantha* H. L. Clark, *aestuarii* (Matsumoto), *vadicola* (Matsumoto), *decacantha* H. L. Clark, *tenuis* H. L. Clark, *heptacantha* Mortensen, *iranica* Mortensen and *africana* Balinsky. The second category consists of species with *Amphioplus* (D)-type oral papillae, namely *stewartensis* Mortensen, *magellanica* Mortensen, *Amphioplus cyrtacanthus* H. L. Clark, 1915, *A. lucidus* Koehler, 1922a, *A. seminudus* Mortensen, 1940 and doubtfully *A. luctator* Koehler, 1922a, the last four having been referred to it by Fell (1962a) (and not having been previously mentioned in this paper merit the fuller details). In 1955 I myself named some discless West African specimens " *?Ophionephthys* sp.", noting, however, that although they are probably congeneric with *O. magellanica* and *stewartensis*, the same could not be said of their relationship with *O. limicola*.

Of the species in the first category, Fell removed all except *phalerata* and *tenuis* (which he included in *Ophionema*) to *Ophiopeltis* ; I am now transferring those two also to *Ophiopeltis* but simultaneously abstracting to the new subgenus *Fellaria* six of the others—*ecnomiotata*, *octacantha* (with synonym *decacantha*), *vadicola*, *heptacantha* and *africana*.

In his revised diagnosis of *Ophionephthys* (1962a : 15), Fell gives the number of oral papillae as four or five (i.e. of the *Amphioplus* (D)-type) and used the genus as a repository for several species of *Amphioplus* the type-specimens of which were lacking the disc, arousing the supposition that their disc scaling was reduced. However, a number of amphiurids with fully-scaled discs also frequently shed or otherwise lose them. Anyway the figures of Nielsen (1932) and Thomas (1962) as well as some specimens kindly sent to me by Dr. Thomas show that Fell's description of the mouth parts is incorrect and that *Ophionephthys limicola* has oral papillae arranged unlike those of any of the major genera of Amphiurids. However, it would be remiss not to point out that occasional specimens, particularly some immature ones, of a few species of *Amphioplus* like *A. strongyloplax* (fig. 9b) and *macraspis* (both originally described as species of *Amphiodia* by H. L. Clark, 1911) may lack the fourth oral papilla from the adoral shield ; but then the third papilla, as often in *Amphioplus*, arises from the point of junction of the oral plate and the adoral shield, not from the oral plate alone as in *O. limicola*, the oral formula in these two species of *Amphioplus* being $\text{m,m}\overset{\frown}{\text{n,n}}\text{m}$ +t or $\text{m,m}\overset{\frown}{\text{n,n}}\text{o}$ +t. The presence of the oral tentacle scale of course distinguishes both *Ophionephthys* and *Amphioplus* from *Amphiodia*.

Of the second category of species, i.e. those referred to *Ophionephthys* by Fell, only the types of *Amphioplus seminudus* were in possession of their discs ; these have scales present only around the proximal end of each pair of radial shields, the rest of the disc being naked. However, Castillo (1968) has recently discovered additional material of *Ophionephthys magellanica* from southern Chile, which he says show fully-scaled discs so that the species is undoubtedly referable to *Amphioplus*. It may be noted that Chang (1948) has figured a specimen with the disc fully-scaled above but naked below under the name of *Amphioplus cyrtacanthus* but this does not appear to have the arm spines hooked, unlike the holotype, and I think the identification needs confirmation. The three other species, *lucidus*, *luctator* and *stewartensis* also await the discovery of intact specimens ; meanwhile I am sure their affinities lie with *Amphioplus*.

There is, however, one species normally included in *Amphioplus* which appears to have some affinity with *Ophionephthys limicola* ; this is **Amphioplus coniortodes** H. L. Clark, 1918, also from the West Indian area. The holotype (fig 9d, e) has the oral formula m,(m = t)mm,o in most series, with three papillae on the side of the oral plate, the proximal-most of these being very slightly higher and clearly homologous with the oral tentacle scale of other species. The outermost papilla does not seem to me to make contact with the adoral shield although H. L. Clark describes it otherwise. In some series there is a very small papilla on the side of the first ventral arm plate in series with the rest giving a formula of m,(m = t)mm,,m. This arrangement shows some difference from the specimen figured by Thomas (1962, fig. 10B) which has the more usual *Amphioplus* (D)-type formula m,(m = t)mm,m, while one of the four series drawn even has a second papilla on the edge of the adoral shield. The disc of *A. coniortodes* also tends to approximate to that of *O. limicola*, being covered with naked skin below while the dorsal scaling is extremely fine (so much so in the holotype as to be barely distinguishable). In addition there is an enlarged series of scales extending interradially from each radial shield, something like the line of scales in *O. limicola*. Finally, *A. coniortodes* also has extremely long arms, equal in length to about twenty times the d.d. Thomas has pointed out that the two species are commonly associated in the same soft mud in Florida, so some of the resemblances between them may be convergent. Fell (1962a) has referred *A. coniortodes* to his new nominal genus *Ailsaria*, together with several other species of *Amphioplus* with more or less reduced disc scaling. This is dealt with below under the heading of *Amphioplus*.

AMPHIURA (cont.)

Amphiura correcta Koehler

fig. 4a, b

Amphiura correcta Koehler, 1907 : 300–301, pl. 12, figs. 30, 31.
Amphiura norae Benham, 1909 : 104, figs. 1–3 ; Fell, 1958 : 26–27.
Amphiura abernethyi Fell, 1951 : 1–3, figs. 1–4.

Among the specimens studied by me at the Museum of Comparative Zoology, Harvard in 1954 was a syntype of *Amphiura correcta,* the locality of which was unknown although the types were collected by Quoy and Gaimard on the voyage of Dumont d'Urville (on the " Astrolabe " primarily to Australia, New Zealand and the South Seas). This specimen (fig. 4a, b) proved to be conspecific with *Amphiura norae* Benham from New Zealand. The same is true of a syntype of *A. abernethyi* sent to the British Museum by Dr. Fell in 1952, which indicates that Fell's drawings over-exaggerated the peculiarities such as the shape of the radial shields and the scales between them ; the latter are simply rounded in the syntype sent to me ; also there is a suture separating oral plates and adoral shields each side of the apex of the oral shield so that the two adorals are not contiguous, the oral shields themselves are more nearly hexagonal than rhombic, the distal oral papilla is broad rectangular or fan-shaped and the dorsal arm plates have the distal side with a median convex angle and are not simply curved. The fifth arm spine found in *abernethyi* compared with the four counted by Benham can be attributed to the much larger size of the types of the former. In a letter of November, 1952, Dr. Fell agreed with me that *norae* and *abernethyi* could be " lumped together ", having studied a further range of specimens which indicated to him that a single variable species is present. However, in his paper of 1958 he mentioned this synonymy as only a possibility.

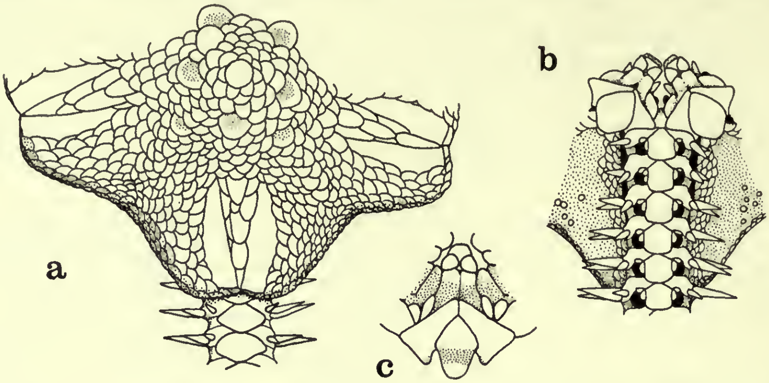


Fig. 4. a and b. *Amphiura correcta* Koehler, M.C.Z. 1303, syntype, locality ? (presumably New Zealand) ; c. *A. lorioli* (Koehler), 1948.5.26.69 (pt.), paratype of *A. ceramis* H.L.C., Zanzibar area, one jaw.

Amphiura lorioli (Koehler)

fig. 4c

Ophiactis lorioli Koehler, 1897 : 328 ; 1899 : 41–42, pl. 6, figs. 46, 47.
Amphioplus lorioli H. L. Clark, 1915 : 258 ; 1918 : 295 ; Fell, 1962a : 17.
Amphiura ceramis H. L. Clark, 1939 : 58–60, figs. 14, 15.

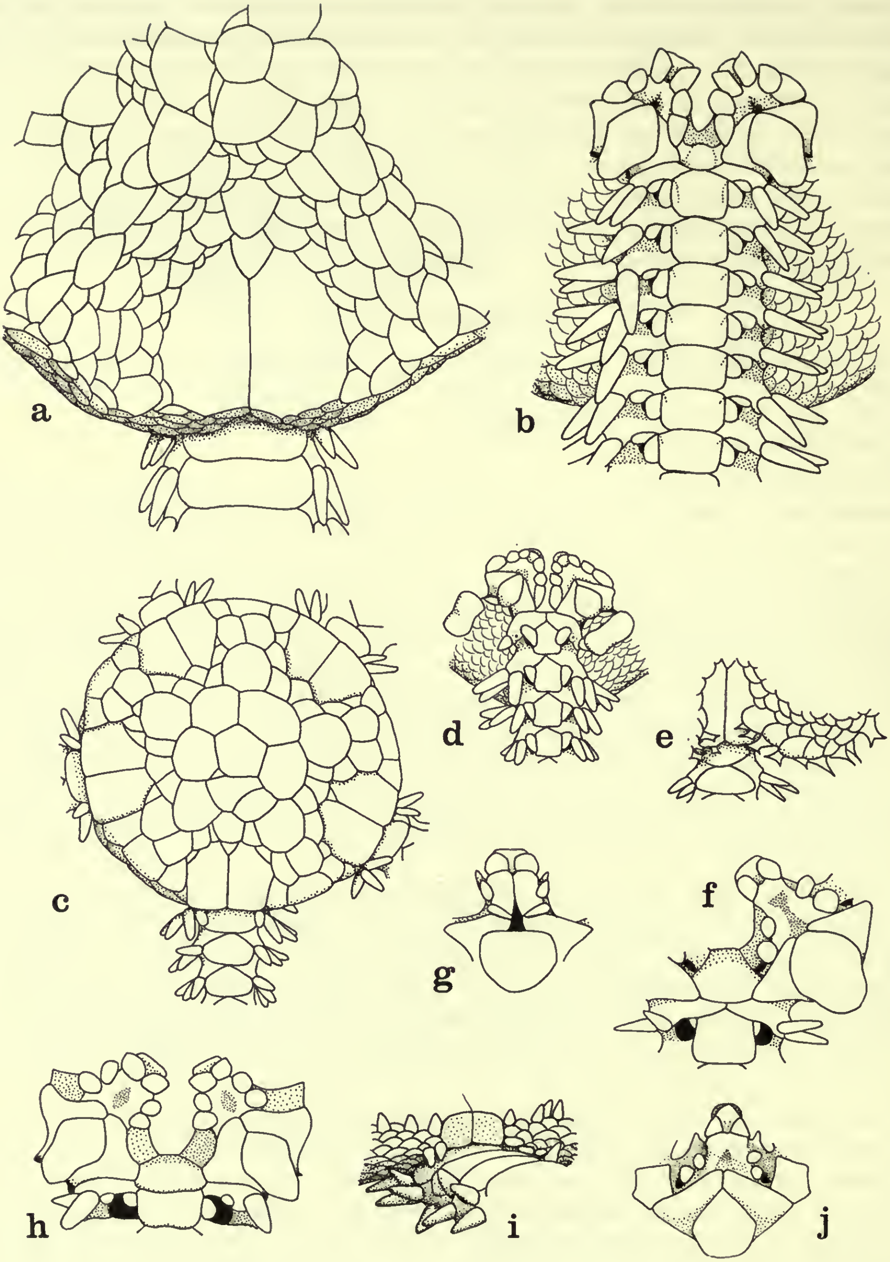
The holotypes of both *Ophiactis lorioli* and *A. ceramis* are in the British Museum collections. Comparison reveals no significant difference. Both have extremely large and few disc scales for an amphiurid and unusually small oral shields with the constricted though elongated distal lobe markedly depressed and a close pair of distal oral papillae each side. The oral formula is m,om,,m +t (or m,o$\overparen{\text{n,n}}\overparen{\text{n,n}}$ +t), the distal papillae, though close together, hardly abutting at all on the edge of the adoral shield (as H. L. Clark's figure incorrectly shows them, though his description is better ; the teeth are also broader than his figure shows). There is some resemblance in the oral structure to *Ophiomonas* though the oral tentacle scale is rather deeper in the slit basally in *A. lorioli*. The paratypes of *A. ceramis* are remarkably variable in the number and arrangement of their oral papillae ; one even has a formula of m,omm,m$\overparen{\text{n,n}}$ +t in five series but m,om$\overparen{\text{n,n}}\overparen{\text{n,n}}$ +t in the other five, thus illustrating the close relationship of *Amphiura* with *Amphioplus*.

AMPHIODIA Verrill

Amphiodia Verrill, 1899a : 306, 313 ; 1899b : 25 ; H. L. Clark, 1915 : 245 ; Nielsen, 1932 : 267 ; Djakonov, 1954 : 61 ; Fell, 1962a : 5, 15 ; Thomas, 1962 : 640 ; 1964 : 164–165. Type-species : *Amphiura pulchella* (Lyman, 1869).
Amphiodia (*Amphispina*) Nielsen, 1932 : 276.
[See also p. 25 for synonyms.]

The Amphiurid species with *Amphiodia* (B)-type jaw armament and unarmed discs exhibit a much narrower range of form with regard to other characters than those of the (A)-type. In none of the species so far described does the disc lack scales on the upper side, though they may be naked below, also tentacle scales are never lacking altogether and the number of arm spines rarely exceeds five. Accordingly Fell (1962a) could only split the genus into three using his criteria of disc scaling and tentacle scale number, dividing off *Gymnodia* with the disc skin-covered below from *Amphiodia* and *Diamphiodia* with fully-scaled discs and one or two tentacle scales respectively. (Evidently he suffered a change of mind about the new nomenclature involved, since the name *Ailsaria* appears in his key in the proper place for *Gymnodia*, judging from the diagnoses, while the nomen nudum *Gymnoplus* takes the place of *Ailsaria*.)

The type-species of *Amphiodia*, **Amphiodia pulchella** (Lyman, 1869) has been fully described and figured by Thomas (1962) who points out that the ventral scales " may be difficult to see unless the specimen is dried ". Accordingly Thomas refers *Amphiura repens* Lyman, 1875 (included by Fell in *Gymnodia*), to the synonymy of *A. pulchella*. The type-species of **Gymnodia, Amphiodia tabogae** Nielsen, 1932, is evidently very variable. The second specimen figured by Nielsen (1932, fig. 10a and c, p. 273) appears very similar to *Amphiodia pulchella* and I fully agree with Thomas (1964) that there cannot be a generic distinction between them. Of the other two nominal species referred to *Gymnodia*, **Amphiodia platyspina** Nielsen, 1932 is very similar to *A. tabogae*, differing mainly in the modification of some of the middle arm spines, while *Amphiodia psilochora* H. L. Clark, 1911 (fig. 5g) has the oral tentacle scale present and so does not belong to the *Amphiodia* (B)-group at all ; it resembles an *Amphioplus* with the distalmost oral papilla suppressed as may occur in *A. coniortodes* already mentioned (p. 21) ; I have also observed some scattered scales in the ventral interradii of the holotype of *A. psilochora*. Nielsen has also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noted that in larger specimens (d.d. up to 11 mm. in his material) of **Amphiodia occidentalis** (*Diamphiodia* according to Fell) " the scales in the proximal part of the ventral interradii are resorbed, so that the skin of the disc is transparent on specimens in alcohol ". It should also be mentioned that **Amphiodia obtecta** Mortensen, 1940, which Fell left in *Amphiodia*, has the ventral side of the disc naked ; Mortensen also commented that specimens in alcohol appear to be naked above as well but drying reveals the scales on the dorsal side. In face of these observations it seems impossible to accept variations in disc scaling as providing characters of generic or even subgeneric weight in this context.

As for tentacle scale number, supposed to characterize **Diamphiodia**, at least one species of *Amphiodia*, **Amphiodia euryaspis** H. L. Clark, 1911, has either one or two scales, as I found on studying the type-material in the Smithsonian Institution. Here again I cannot accept this as a generic character. Accordingly the following are here referred to the synonymy of *Amphiodia* Verrill, 1899:

Gymnodia Fell, 1962a (type-species *Amphiodia tabogae* Nielsen, 1932).
Diamphiodia Fell, 1962a (type-species *Amphiura violacea* Lütken, 1856).

Nielsen's subgenus *Amphispina* (1932), for which no type-species was designated by Nielsen, is strictly speaking a nomen nudum on that account under Article 13b of the Code of Nomenclature. I cannot trace a subsequent type-designation and since I consider that *Amphiodia* (*Amphispina*) *digitata* Nielsen, 1932, together with *Ophiophragmus duplicatus* Koehler, 1930 and *Amphiodia microplax* Burfield, 1924, form a natural group distinguished by the spiniform prolongations of the uppermost row of ventral disc scales, it is necessary to re-establish the name as follows:

AMPHIODIA subgenus *AMPHISPINA* nov.

Amphiodia (*Amphispina*) Nielsen 1932: 276–277.

TYPE-SPECIES. *Amphiodia* (*Amphispina*) *digitata* Nielsen, 1932.

DIAGNOSIS. A subgenus of *Amphiodia* distinguished by the modification of the uppermost row of ventral disc scales with the free edges prolonged into single or forked spines.

FIG. 5. a and b. *Amphiodia psara* H.L.C., M.C.Z. 965, holotype, Corona del Mar, California; c and d. *Amphiodia crassa* Koehler, U.S.N.M. 40953, " Albatross " st. 5282, Philippine Is. (d.d. only 2·5 mm ; in d the two giant arm spines of the first segment of the arm drawn are both lost but those of the adjacent arms are shown) ; e and f. *Amphiodia* (*Amphispina*) *duplicata* Koehler, 1949.8.15.24, paratype, Amboina, e showing spinose projections of marginal scales, f relatively more enlarged to show details of oral structure ; g. " *Amphiodia* " *psilochora* H.L.C., U.S.N.M. 25544, holotype, Sagami Bay, Japan, showing the oral tentacle scale in contrast with f ; h. *Ophiophragmus wurdemanni* Lyman, M.C.Z. 1119, holotype, Charlotte Harbour, Florida ; i. *O. brachyactis* H.L.C., M.C.Z. 1120, holotype, off Sombrero Key, Florida, side view of base of arm showing marginal papillae fringing the distal edge of the large radial shields with a few additional papillae just above the arm base each side ; j. " *Amphiodia* " *affinis* (Studer), 1936.12.30.769, South Georgia.

I do not agree with Nielsen that **Amphiodia urtica** (Lyman, 1860) should be referred to the subgenus *Amphispina* ; it has many or all of the ventral disc scales angular or with spinose more or less projecting points on the free edges and possibly merits a separate supraspecific distinction comparable with *Acrocnida* of the *Amphiura*-group. Fell (1962a) mistakenly refers it to *Ophiophragmus* although it lacks articulated marginal papillae.

AMPHIODIA sensu extenso (cont.)

Of the forty-seven nominal species included in *Amphiodia, Diamphiodia* and *Gymnodia* by Fell (1962a), a large number are from east or west America (excluding Alaska and Chile), namely *Amphiodia atra* (Stimpson, 1852) (referred to *Micropholis* nov. by Thomas, 1966 and with synonyms *Ophiolepis limbata* Grube, 1857 and *Amphiodia gyraspis* H. L. Clark, 1915, according to Thomas, 1964), *A. grisea* (Ljungman, 1867b), *A. occidentalis* (Lyman, 1860), *A. oerstedi* (Lütken, 1856), *A. peloria* Bush, 1921, *A. periercta* H. L. Clark, 1911, *A. planispina* von Martens, 1867, *A. platyspina* Nielsen, 1932, *A. psara* H. L. Clark, 1935, *A. pulchella* (Lyman, 1869) (with synonym *Amphiura repens* Lyman, 1875, according to Thomas, 1962), *A. riisei* (Lütken *in* Lyman, 1860), *A. sculptilis* Ziesenhenne, 1940, *A. tabogae* Nielsen, 1932, *A. trychna* H. L. Clark, 1918 (with synonym *A. tymbara* H. L. Clark, 1918, according to Thomas, 1962), *A. vicina* H. L. Clark, 1940 and *A. violacea* (Lütken, 1856). To these can be added *A. urtica* (Lyman, 1860) with synonym *Amphiura barbarae* Lyman, 1875, according to Nielsen (1932).

More than half of these species, namely *A. grisea, oerstedi, planispina, platyspina, psara* (fig. 5a, b), *riisei, sculptilis, tabogae, trychna, vicina* and *violacea*, show a more or less marked tendency for broadening of the third oral papilla, which may approximate in proportions to the operculiform third papilla of *Amphipholis* sensu extenso, witness the uncertain position of *Ophiolepis atra* Stimpson, transferred to *Amphipholis* by Ljungman, 1867, to *Amphiodia* by Verrill, 1899 and back to a newly-formed division of *Amphipholis* by Thomas, 1966. In addition, a number of the American species of *Ophiophragmus*, such as *O. brachyactis* H. L. Clark, 1915, *O. luetkeni* (Ljungman, 1871), *O. marginatus* (Lütken, 1859), *O. paucispinus* Nielsen, 1932, and *O. pulcher* H. L. Clark, 1918 (but not *O. wurdemanni* (Lyman, 1860), the type-species), also share this tendency. Since Thomas (1962) has found the holotype of *Amphiodia rhabdota* H. L. Clark, 1918 to be a specimen of *Ophiophragmus pulcher* deficient in the marginal papillae supposedly characteristic of the genus *Ophiophragmus*, I think that similar synonymies will also be discovered among some of the other nominal species, for instance *Amphiodia violacea, A. psara* (fig. 5a, b) and *O. marginatus* would bear comparison and indeed the supra-specific limits between the species of *Amphiodia* and *Ophiophragmus* named above, together with most of the American species of *Amphipholis* sensu extenso, especially those which Thomas (1962) has referred to his new nominal genus *Micropholis* (namely *Amphipholis atra* (Stimpson, 1852), *gracillima* (Stimpson, 1852), *subtilis* Ljungman, 1867b, *platydisca* Nielsen, 1932, *geminata* (Le Conte, 1851) and *puntarenae* (Lütken, 1856), are badly in need of revision. It is to be hoped that Thomas will go fully into this matter in his monograph of west Atlantic amphiurids (now in course of preparation), though it is unfortunate that the compass of this work apparently excludes the many closely-related species described from the western coasts of America.

The abstraction of the species of *Amphiodia* with the third papilla enlarged leaves only four American species with three approximately equal oral papillae on each half of the jaw, namely *A. pulchella*, *A. occidentalis*, *A. periercta* and *A. peloria*. Out of the 25 nominal species remaining which Fell referred to *Gymnodia*, *Diamphiodia* and *Amphiodia*, only eight more appear to me to be valid species of *Amphiodia*. These are *A. craterodmeta* H. L. Clark, 1911, *A. crassa* (Koehler, 1904) (fig. 5c, d), *A. dividua* Mortensen, 1933c, *A. euryaspis* H. L. Clark, 1911, *A. fissa* (Lütken, 1869), *A. frigida* (Koehler, 1897), *A. minuta* H. L. Clark, 1939 and *A. obtecta* Mortensen, 1940, to which may be added *A. debita* Koehler, 1922a and *acutispina* Koehler, 1914, of the three which Fell mentioned as incertae sedis. The remainder are disposed of as follows: **Amphiodia psilochora** H. L. Clark, 1911 (fig. 5g) has an oral tentacle scale (as mentioned above, p. 23) and resembles an *Amphioplus* with the fourth (distalmost) oral papilla suppressed ; its oral formula is m,mm,o +t. It is here provisionally referred to *Amphioplus* and discussed further on p. 57. **Amphiodia affinis** (Studer, 1885), **ochroleuca** (Brock, 1888), **grata** (Koehler, 1904), **reposita** (Koehler, 1905) and **servata** (Koehler, 1904) (see figs 5j and 8 (part)) also have the first oral tentacle scale present but usually have a slight diastema between the infradental and middle papillae (very small in the case of some specimens of *ochroleuca*—see fig. 8t) and the distalmost papilla is based at least partly on the edge of the adoral shield (except in *affinis* where both the distal papillae are usually inset somewhat on to the oral plates though there is a great deal of variation in their number and arrangement); the formula for most of these species can be expressed as m,om,m +t and they are referred to subdivisions of *Amphioplus* as stated on pp. 48 and 49. **Amphiodia assimilis** (Lütken & Mortensen, 1899) and **caulleryi** (Koehler, 1897), judging from the respective figures, resemble species of *Amphiura* with two distal oral papillae, having a large diastema at the side of the oral plate and the two distal papillae forming a symmetrical pair each side based on the adoral shield ; their formula may be given as m,o,mm +t, possibly m,o$\overset{\frown}{n,n}$m +t, much as in *Amphiura filiformis*, with which I believe they are congeneric. (See also p. 43). **Amphiodia digitula** H. L. Clark, 1911 is another such species and I agree with Djakonov (1954) in referring it to *Amphiura*. **Amphiodia olivacea** (Brock, 1888) has short blunt marginal spines and should be referred to *Ophiophragmus*, while **Amphiodia fuscoalba** (Brock, 1888) (the third of Fell's species incertae sedis) appears from the description to have *Amphiura* (A)-type oral papillae and granuliform scales on the underside of the disc ; it may therefore be referred to *Acrocnida*. **Ctenamphiura sinensis** A. H. Clark, 1917, which Fell rather incomprehensibly placed in *Diamphiodia* despite its four oral papillae more like *Amphioplus*, I have recently (1967) referred to *Paracrocnida*. Similarly **Amphioplus brachiostictus** Tortonese, 1949 has four oral papillae and cannot therefore be included in *Amphiodia*. However, Mortensen (1952) mentions it as being similar to *Amphiodia chilensis* (Müller and Troschel), which he maintains is better-placed in *Amphiodia* than in *Ophiophragmus* although some specimens of it have marginal papillae. Three of the four remaining names are synonyms, **Amphiodia antarctica** (Ljungman, 1867b) of *A. chilensis* (Müller & Troschel, 1842), according to Mortensen (1936), **A. rhabdota** H. L. Clark, 1918 of *Ophiophragmus pulcher* H. L. Clark, 1918, according to Thomas (1962) and **A. rossica** Djakonov, 1935 of *A. fissa* (Lütken, 1869), according to me (1965). Finally, **Amphiodia cyclaspis** (originally *cyclospis*), also of Djakonov, 1935, was clearly based on a specimen with incompletely-regenerated disc, which accounts for the supposedly diagnostic characters of the diminutive separated radial shields and the mosaic of small plates on the upper side of the basal arm segments ; Djakonov compared it otherwise with the sympatric *A. craterodmeta*, with which I suggest it is synonymous. Djakonov (1954) gives a figure of the dorsal side but the ventral has never been illustrated.

OPHIOCNIDA Lyman

Ophiocnida Lyman, 1865 : 133 ; 1882 : 152–153 ; Verrill, 1899b : 315–316 (sensu Lyman), p. 317 (restricted) ; H. L. Clark, 1915 : 250 ; Thomas, 1962 : 683–684. Type-species : *Ophiolepis hispida* Le Conte, 1851 (designated by Verrill, 1899b : 317).

Ophiocnidella Ljungman, 1871 : 649. Type-species : *Amphiura scabriuscula* Lütken, 1859.

Ophiocnida hispida, the type-species, has oral papillae of the *Amphiodia* (B)-type (fig. 7c). The same is not strictly true of one of the other species which is currently still included in *Ophiocnida*, having been referred to it by Lyman (1874), namely *Ophiophragmus echinatus* Ljungman, 1867b. This species has *Amphioplus* (D)-type oral papillae (fig. 7k), as least when mature, and accordingly with its spinose disc is now referred to the genus hitherto known as *Amphiacantha* Matsumoto, 1917 for which a new name is proposed on p. 33.

Another species is a doubtful member of the genus *Ophiocnida*, namely *O. loveni* (Ljungman, 1867a), for further mention of which see p. 31.

AMPHIPHOLIS Ljungman

Amphipholis Ljungman, 1867a : 165 ; 1867b : 311–312 ; Verrill, 1899a : 24 ; 1899b : 306, 311–312 ; H. L. Clark, 1915 : 240 ; Djakonov, 1954 : 64 ; Fell, 1962a : 15 ; Thomas, 1962 : 657 ; 1966 : 827–833. Type-species : *Amphipholis januarii* Ljungman, 1867a.

[See below, p. 31 for synonyms.]

As with *Amphiodia*, the Amphiurid species with *Amphipholis* (C)-type jaw armament and unarmed discs exhibit a fairly narrow range of form in comparison with *Amphiura* with regard to disc scaling, though their tentacle scales may be reduced to one or (in one case) totally absent. Fell (1962a) was thus able to divide off only *Monopholis* with one tentacle scale and *Nullopholis* with none from *Amphipholis* restricted. As Thomas (1966) has pointed out, the second species which Fell refers to **Nullopholis, Amphipholis pentacantha** H. L. Clark, 1915, has tentacle scales present on the basal segments (in fact there are two on several pores of the very first segments though only one on the next two segments, the remaining pores having none, see fig. 6e, f). (Similarly *A. murmanica* Djakonov, 1929 loses its single scale distally.) Thomas also notes that *A. pentacantha* is not at all closely related either to *Amphipholis nudipora* Koehler, 1914 the type-species of *Nullopholis*, or to *A. vitax* (Koehler, 1904), the type-species of **Monopholis**, being isolated from them both by its very coarse disc scaling and from *nudipora* also by its relatively numerous and elongated arm spines. Djakonov (1954) notes that *A. murmanica* is closely related to *A. squamata* except for having only a single tentacle scale, while the one remaining species referred to *Monopholis* by Fell, *A. loripes* Koehler, 1922a (fig. 6a), is known only from a single discless specimen and appears to have some affinities with *Amphiodia*. Certainly the three species do not form a natural group and I can see no justification for separating them off from *Amphipholis*. Nor can I find other characters to support the absence of tentacle scales in *A. nudipora* to warrant its separation and I fully agree with the rejection of these two nominal genera. However, Thomas himself proceeds to divide up the species of *Amphipholis* on different criteria, most notably the shape of the oral plate in side view and the occurrence of perforations through the arm ossicles. The observation of both these characters requires dissection and special preparation ; also their use as taxonomic characters is of recent introduction, the study of oral plates being initiated by Murakami (1963) (discounting his preliminary paper of 1947 in Japanese) and of arm ossicles by Buchanan & Woodley (1963). Although Murakami covered a fair number of Japanese species, these included only a few from each of the larger genera, four of *Amphipholis* for instance, while only two species of *Amphiura*, *filiformis* and *chiajei* have had their arm ossicles described with regard to this character, apart from Thomas's summarized remarks for his subdivisions of *Amphipholis*. The perforation of the arm ossicles appears to be correlated with the degree of extension of which the tube feet are capable and this appears to depend on the feeding habits of the animals. Evidently in *Amphipholis januarii* the distal (more immature) arm ossicles may be perforated but not the proximal ones ; so there is also a chance that this is an ontogenetic rather than a functional modification. Much more work is clearly needed on the functional morphology of a wide range of species of Amphiurids before it can be determined to what extent the sharing of perforated ossicles is attributable to convergence of habit. Since Thomas is now engaged on such a study, it is obviously premature to take decisive action here with regard to his new taxa. More details are needed to render the preliminary distinction of these convincing.

The diagnoses Thomas gives for these three nominal genera can be summed up in the form of a table:

	Amphipholis	*Axiognathus*	*Micropholis*
Oral papillae able to close slit	almost	+ or almost	almost
Tentacle scales	2	1 or 2	2
Arm spines	4	3–5	3–5
2nd spine modified	+	—	—
Successive dorsal arm plates contiguous	just	—	+
Arm ossicles perforated	only distally	—	+
Oral plates with strong abradial wings	+	—	+
Disc scales	“ prominent ”	“ large ”	“ small ”
Radial shields	not stated but joined for c. 2/3	“ joined their whole length ”	not stated but +/— contiguous

In the case of *Amphipholis* restricted, the diagnosis is derived from only a single species and in *Axiognathus* from four. Certainly most of the characters involved are only of specific weight, apart from the two already mentioned, the importance of which remains to be seen, while it is just possible that modification of the second arm spine will prove to allow a supra-specific grouping, though below the generic level unless supported by other characters. Superficially the differences between *Amphipholis januarii* (fig. 6b–d) and *A. squamata,* the type-species of *Amphipholis* and *Axiognathus* respectively, are very slight and considerable evidence will be needed to convince me that they are generically distinct.

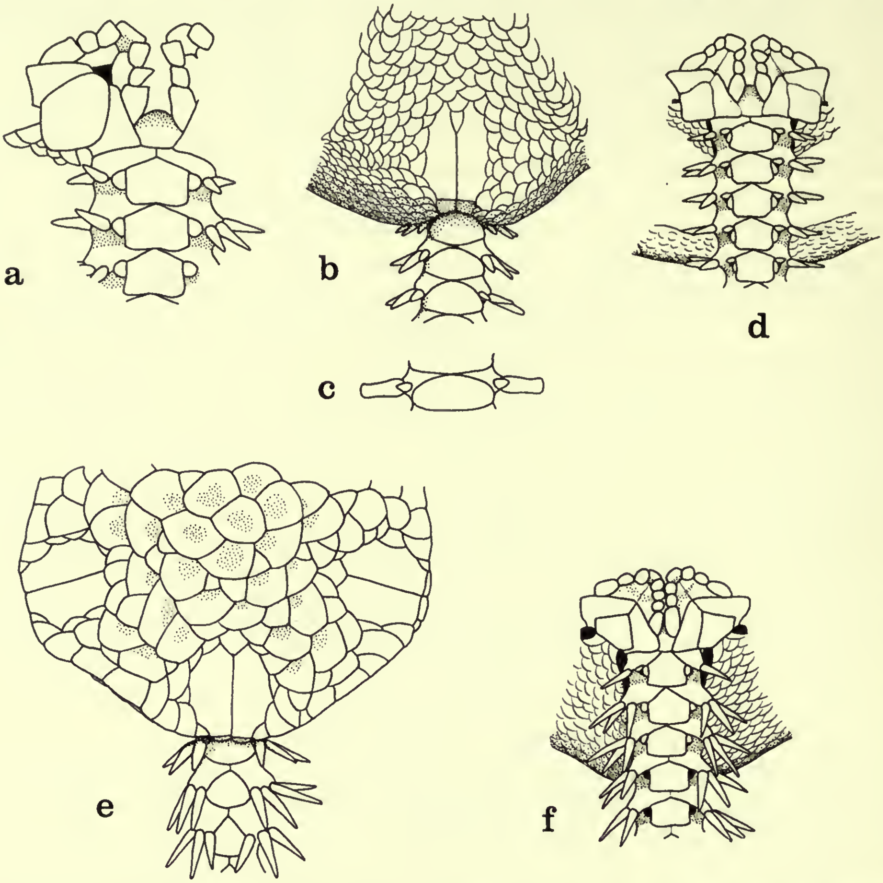


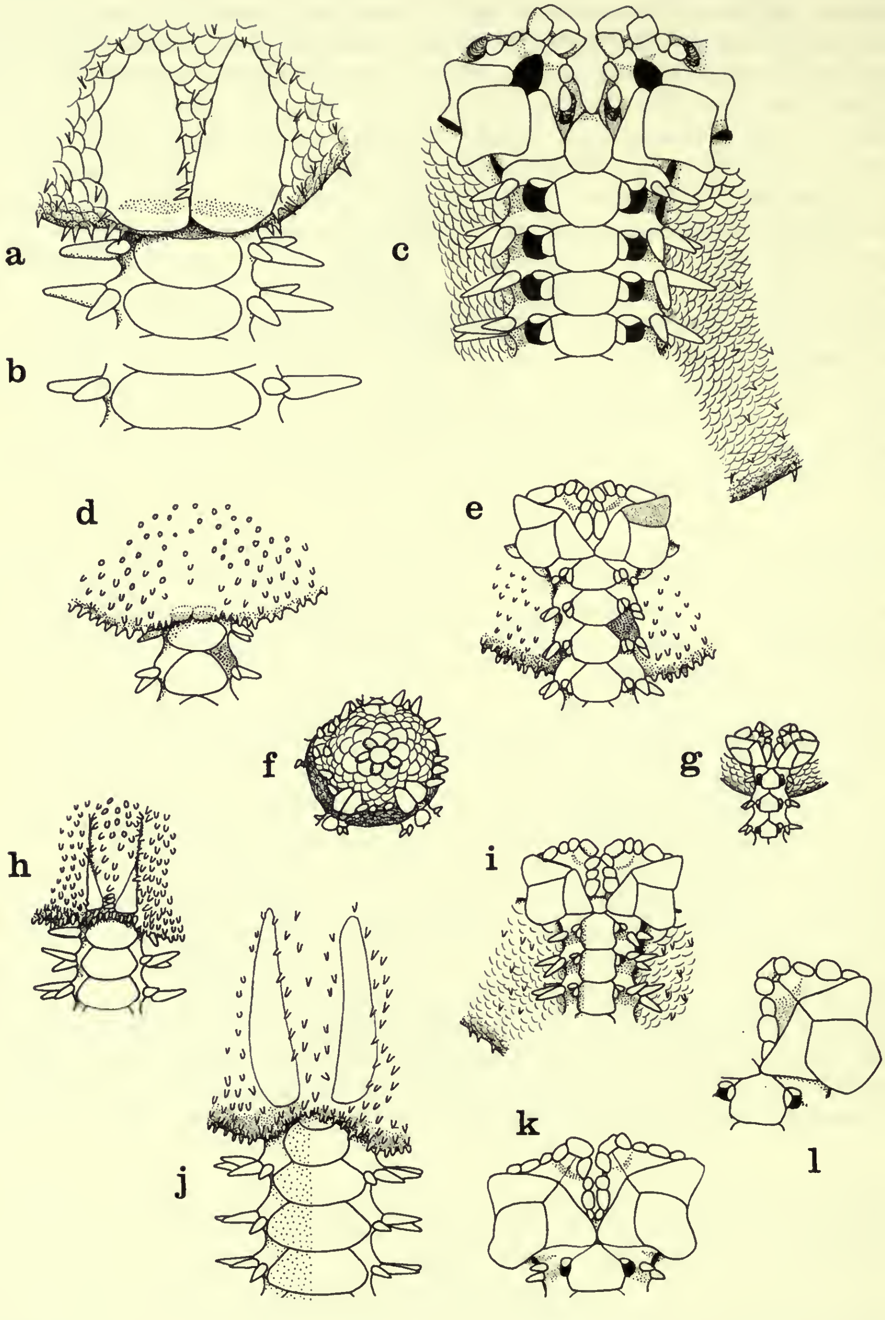
Fig 6. a. *Amphipholis loripes* Koehler, U.S.N.M. 41190, holotype, " Albatross " st. 5375, Philippine Is. (only a few disc scales remain attached to the oral shields but enough to show that the disc was not naked below) ; b–d. *A. januarii* Ljungman, M.C.Z. 4140, holotype of *A. pachybactra* H.L.C., Buccoo Bay, Tobago, c shows the thirtieth arm segment from above (all the ventral interradii are ruptured, hence the gaps in d) ; e and f. *A. pentacantha* H.L.C., M.C.Z. 1437, holotype, off St. Lucia, West Indies.

Inevitably my reluctance to accept this schism is increased by desire to retain the familiar combination **Amphipholis squamata** (Delle Chiaje, 1829) for this the most nearly cosmopolitan echinoderm of all and one which must feature on a great number of fauna lists, so that a change of generic name would cause extensive confusion. However, after scrutinizing the literature I cannot find any explanation why the specific name *squamata* has been used since 1900 in face of the obvious priority of *Ophiura elegans* Leach, 1815. Leach's short description and more particularly his notes that the disc scales are " of nearly one size and the margin has a distinct row of scales running round it ", together with the drab colour and the locality on the rocks in South Devon, convince me that his material was conspecific with *A. squamata*. If the latter name is to be retained, then some approach is needed to the International Commission on Zoological Nomenclature to request that the plenary powers be exerted to reject *O. elegans* Leach formally and validate *O. squamata* Delle Chiaje. Simultaneously I would have liked to be able to recommend that the usage of *Amphipholis* in Ljungman's preliminary paper (1867a) be suppressed in order to validate that in his main paper (1867b), where the first-named and best-known species included is *A. elegans* (Leach) with *squamata* given as a synonym. [A type-designation of *A. squamata* has already been given by Verrill (1899a : 24 and 1899b : 306, but not p. 311 which names *januarii*).] However, it is difficult to justify *squamata* as type-species in face of Ljungman's treatment of the genus.

Accordingly I propose to suspend consideration of the adoption of *Axiognathus* and *Micropholis* pending publication of Thomas's monograph ; meanwhile I hope for some response by interested parties to my proposals for stabilizing the specific name *squamata*. At present therefore, *Amphipholis* is treated in the wide sense with only the following synonyms:

Nullopholis Fell, 1962. Type-species : *Amphipholis nudipora* Koehler, 1914.
Monopholis Fell, 1962. Type-species : *Amphiura vitax* Koehler, 1904.

In addition to the species listed by Fell, there are two others which have been referred to *Amphipholis*. One of these is *A. tetracantha* Matsumoto, 1941, from Japan and the other **Amphiura murex** Koehler, 1908, from Brazil. The holotype of the latter is relatively small (d.d. only 2·5 mm.) and has the under side of the disc covered with conical granules while the upper side has relatively large naked scales. This unusual combination is shared by **Ophiocnida loveni** (Ljungman, 1967a), also known from Brazil, of which I believe *A. murex* is a synonym. I am uncertain whether *O. loveni* is congeneric with the type-species of *Ophiocnida*, *O. hispida* (Le Conte, 1851), the latter having the disc scales distinct on both sides and with small spinelets scattered all over. The affinities of *O. loveni* appear to be more with *Amphichondrius granulosus* Nielsen, 1932 or *Ophiophragmus filograneus* (Lyman, 1875), once also included in *Ophiocnida*.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OPHIOSTIGMA Lütken

Ophiostigma Lütken, 1856 : 13 ; 1859b : 233 ; Lyman, 1865 : 103 ; Ljungman, 1867b : 317 ; Lyman, 1882 : 164–165 ; H. L. Clark, 1915 : 243 ; Fell, 1960 : 22 ; Thomas, 1962 : 689. Type-species : *O. tenue* Lütken, 1856, by monotypy.

In 1960 Fell referred *Amphistigma* H. L. Clark, 1938, to the synonymy of *Ophiostigma*, being evidently misled by H. L. Clark's figure of the disc of *A. minuta*, the type-species, which is not very clear. Another figure of the holotype of *A. minuta* is given here (fig. 7f, g) which I hope shows up more conspicuously the marked difference in the disc in comparison with *Ophiostigma*, though certainly both have oral armament of the *Amphipholis* (C)-type. **Ophiostigma tenue** (fig. 7d, e) has papilliform spinelets scattered all over both sides of the disc, whereas in *Amphistigma minuta* there are only a few relatively very large papillae restricted to the margin of the disc while in the centre the five approximately radial scales of the rosette are extremely thickened and projecting but do not bear articulated papillae.

Amphistigma minuta H. L. Clark

fig. 7f, g

Amphistigma minuta H. L. Clark, 1938 : 245–247, fig. 16.

*DOUGALOPLUS** nom. nov.

Amphiacantha Matsumoto, 1917 : 177–179 ; Nielsen, 1932 : 296 ; Djakonov, 1954 : 57. Type-species : *Amphioplus acanthinus* H. L. Clark, 1911. Non *Amphiacantha* Popofsky, 1904, Protozoa.

Unfortunately the generic name *Amphiacantha* used by Matsumoto is preoccupied, as discovered recently by Miss M. Downey of the U.S. National Museum and communicated to me by Dr. D. L. Pawson, to both of whom I am indebted. The replacement name *Dougaloplus* is therefore proposed for the genus.

Apart from the type-species, the genus also includes *Ophiostigma formosa* Lütken, 1872, *Amphiura gastracantha* and *notacantha* both of Lütken and Mortensen, 1899, *Ophiocnida libera* Koehler, 1907 and *O. amphacantha* McClendon, 1909, all referred to *Amphiacantha* by Matsumoto, who also included a new nominal species **Amphiacantha dividua** and *Ophiocnida sexradia* Duncan, 1887, which I consider are synonymous and referable to *Ophiocomella* (*sexradia* having been transferred in 1963

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* Dougal—a shaggy dog of television fame. Gender: masculine.

Fig. 7. a–c. *Ophiocnida hispida* (Le Conte), M.C.Z. 1496, Hassler Expedition, Panama, b shows the twentieth free segment from above ; d and e. *Ophiostigma tenue* Lütken, M.C.Z. 5712, "Velero" st. 870, Isabel Is., W Mexico (the texturing of the surface is indicated on a few plates) ; f and g. *Amphistigma minuta* H.L.C., M.C.Z. 4983, holotype, Lord Howe I. (the dorsal view slightly oblique) ; h–k. *Dougaloplus echinatus* (Ljungman), h and i. Stockholm Museum collection, holotype, N. Gaspar Strait, E of Sumatra, j and k. B. M. 98.6.30.1, Batavia (Jakarta) ; l. *Amphioplus* (?) *luctator* Koehler, U.S.N.M., Kei Is. Expedition st. 77.

Clark *in* Parslow and Clark). Matsumoto also placed *Amphilimna pentacantha* H. L. Clark, 1911 in *Amphiacantha* ; this species has since been referred to the synonymy of *Amphiacantha amphacantha* by Nielsen, 1932. Subsequent additions to the genus have been *A. transacta* Koehler, 1930 and *A. derjugini* Djakonov, 1949. **Amphiacantha transacta** appears to have multiple apical oral (or dental) papillae and the genital slits bordered with genital papillae unlike other Amphiurids ; it must therefore be a member of the Chilophiurida and should be referred to the Ophiocomidae or possibly Ophiochitonidae. *Amphiacantha derjugini*, however, is certainly congeneric with *Dougaloplus amphacantha*, resembling it in the spiniform two middle oral papillae but differing in the single tentacle scale.

One further species is now referred to the genus, namely **Ophiocnida** (originally *Ophiophragmus*) **echinata** (Ljungman, 1867b), to which Lyman (1874) doubtfully referred a specimen from the Philippines although he thought it differed in two important respects from the holotype. There are two specimens in the British Museum collections from Batavia (Jakarta), Java which agree closely with Lyman's description and figures but again have the same two differences from Ljungman's description. To settle their identity, I requested Dr. P. A. Andersson of the Stockholm Museum to lend me the holotype of *Ophiophragmus echinatus*, which he very kindly did. A description of it is given below but the two supposed differences can be dealt with here. Firstly Ljungman describes the radial shields as almost concealed by the disc spines. This is true to some extent in the holotype, only the distal ends of the radial shields being naked and exposed but it looks to me as if the specimen may have been dried at some time (it is now in spirit) since the disc is rather shrunken and the scaling has distorted considerably, in most cases so as to form a fold coinciding with the radial shield and concealing it for most of its length. In one radius this does not apply but here the scaling around the shields appears to have been scraped free of spinelets so it is not absolutely certain that the naked condition of the shields is natural, though I believe it is. These two shields are very long and thin, equal in length to about half r of the disc. The second character concerns the number of oral papillae ; Ljungman describes only three whereas Lyman found four in his specimen with d.d. 10 mm. (at least 2 mm. larger than the holotype), though in a small specimen, d.d. 4 mm., Lyman notes that there are often only three. In the holotype the first impression is that there are only three papillae but on most of the adoral shields there is a small calcification on the edge distal to the third papilla. At best this " papilla " is inconspicuous and it may be quite lacking ; usually it is angled slightly down into the oral slit and partly concealed by the large third papilla so it is not difficult to see how Ljungman overlooked it.

Besides the two specimens from Batavia there are in the British Museum three from Macclesfield Bank, South China Sea and one from the Great Barrier Reef (recorded by H. L. Clark), all of them I believe conspecific with the holotype of *echinatus*. One Batavia specimen is discless but is similar in size to the other where d.d is 12·5 mm. (fig. 7j, k). Both of them have four oral papillae in each series but the outermost one is distinctly the smallest and sometimes partly overlain by the third. Two of the Macclesfield Bank specimens are also discless, though their d.d. must have been about 7 mm. ; their fourth papilla is developed in most series but often partly overlain. The same is true of the Barrier Reef specimen but this is dried and the fourth papilla has a much rougher texture than the other three. The third Macclesfield Bank specimen has d.d. only 4 mm. and the fourth papilla is just distinguishable in a few series ; clearly its development is progressive with growth and seems to be retarded in comparison with most species of *Amphioplus*, though in 1955 I noted something similar in *Amphioplus congensis*. All three intact specimens have long, narrow, separated and quite bare radial shields, as in Lyman's specimen. I think therefore that *echinatus* is better referred to *Dougaloplus* than left in *Ophiocnida*. Its affinities are probably with *D. formosus* from further north in the China Sea, which resembles it in jaw structure with the two innermost papillae widely spaced to the sides of the lowest tooth, the third papilla the largest and the fourth the smallest ; also both have very broadly contiguous adoral shields. *D. formosus* differs from *echinatus* in having the radial shields short, broad and contiguous.

Dougaloplus echinatus (Ljungman)

fig. 7h–k, ?l

Ophiophragmus echinatus Ljungman, 1867b : 316.
?*Ophiocnida echinata* (*O. longipeda* MS) : Lyman, 1874 : 230–231, pl. 4, figs. 22, 23.
Ophiocnida echinata : Koehler, 1898 : 68, pl. 5, fig. 47 ; 1905 : 32 ; H. L. Clark, 1915 : 250 ; Koehler, 1930 : 113.
?*Amphioplus luctator* Koehler, 1922a : 178–179, pl. 68, figs. 1–3 ; 1930 : 106.

Description. I estimate that the holotype (fig. 7h, i) has the d.d. 8 mm., although Ljungman puts the measurement at 7 mm. The arms are all broken distally ; their length is 70+ mm., probably c. 100 mm. The disc is shrunken and partially detached from some of the arm bases. The scaling is obscured on the upper side by the numerous small, slightly tapering, spinelets, many of which have become displaced and directed almost horizontally, especially across the radial shields where the disc is distorted as described above. On the under side the spinelets are progressively fewer proximally and the scaling is distinct.

The oral shields are widest at about the middle of their length or just proximal to this, the proximal angle is acute and the distal lobe broadly rounded. The length just exceeds the breadth. The adoral shields are very broadly contiguous interradially but have no exposed part extending distal to the lateral angle of the oral shield. Radially they are separated by the very small first ventral arm plate. The innermost oral papilla of each series is offset to the side of the lowest tooth and is not strictly infradental. The second papilla is slightly smaller but the third much larger, though it cannot really be called operculiform as in *Ophiostigma* and *Amphipholis*. As described above the fourth papilla is rudimentary and sometimes appears to be absent ; usually it is partially concealed by the third.

The arms are distinctly convex above and below with the result that the dorsal arm plates appear almost carinate and the ventral arm plates have a broad flattened median area but incline inwards at the sides. The dorsal plates are broad fan-shaped with the widest part towards the distal end and the distal side becomes more or less flattened in the middle beyond the basal segments. The ventral arm plates are approximately quadrangular and about as wide as long, proximally slightly wider than long. The arm spines are slightly tapering and blunt-tipped ; they number four just beyond the disc but this soon falls to three.

The type-locality is 2° 30′ S : 107° 10′ E, Gaspar Strait (between Sumatra and the island of Billiton to the east), 33 metres.

SYNONYMY. I believe that **Amphioplus luctator** Koehler, 1922a, (fig. 7l) known only from specimens from the Philippine area and Kei Islands all lacking the disc, will prove to be a synonym of *D. echinatus*. Although Koehler (1930) recorded both nominal species simultaneously from the Kei Islands, both the (presumably complete) specimens which he referred to *Amphiacantha echinata* were small and the distinctive disc would have served to identify them whereas the discless ones which he named *luctator* would all have been perforce identified from the mouth parts.

AMPHIOPLUS Verrill

Amphioplus Verrill, 1899a : 25 ; 1899b : 306, 314 ; H. L. Clark, 1915 : 251 ; Matsumoto, 1917 : 169–170 ; Djakonov, 1954 : 59–60 ; Fell, 1962a : 6, 16–17 ; Thomas, 1962 : 651. Type-species : *Amphiura tumida* Lyman, 1878.

[See also p. 50 for synonym and p. 56 for diagnosis.]

The majority of species included in *Amphioplus* up to 1962 have two tentacle scales and fully-scaled discs, like the type-species, *A. tumidus* (Lyman, 1878), so Fell's subdivision on the basis of these characters still leaves as many as 59 species in *Amphioplus* as restricted. The remainder Fell distributes between three new nominal genera, *Silax*, *Unioplus* and *Ailsaria*. (The last-named is misplaced in Fell's key as explained under the heading of *Amphiodia*.) *Silax* has the disc fully-scaled but no tentacle scales ; *Unioplus* also has full scaling but one tentacle scale ; while *Ailsaria* has the disc at least partially naked below but two tentacle scales. As with *Amphiodia* and *Amphipholis* sensu extenso, the range of combinations of these two characters is much less than in the species of *Amphiura* sensu extenso. The number of species Fell refers to *Silax*, *Unioplus* and *Ailsaria* is respectively two, twelve and four.

The type-species of **Silax** is **Amphioplus verrilli** (Lyman, 1879) from deep water (down to nearly 5,000 metres) in the West Indies. In the holotype of *A. verrilli* the lowest tooth on three of the jaws is distinctly tricuspid (fig. 8a) and the innermost oral papilla of each series cannot strictly be called infradental since it is offset to the side of the tooth ; however, on the two remaining jaws the lowest tooth is straight-edged and there is a symmetrical, infradentally-placed pair of papillae at the apex of the jaw. The oral plates have a slight horizontal flange level with the base of the first oral tentacle scale and dorsal to the second oral tentacle, rendering the scale almost superficial in comparison with its position deeper in the oral slit in most species of *Amphioplus* including *A. tumidus*. Also, apart from the adapical papilla of each half-jaw, there are only two distal oral papillae (or scales of the second oral tentacle) making a total of three oral papillae, as in *Amphichilus*, not four as in

Amphioplus sensu stricto, the fourth one mentioned by Lyman being the first oral tentacle scale. The oral formula is m,om,m +t (or m,om$\overset{\frown}{n,n}$ +t), though on the half-jaws which have the first oral tentacle scale most nearly superficial it could be written as m,(m = t)m,m.

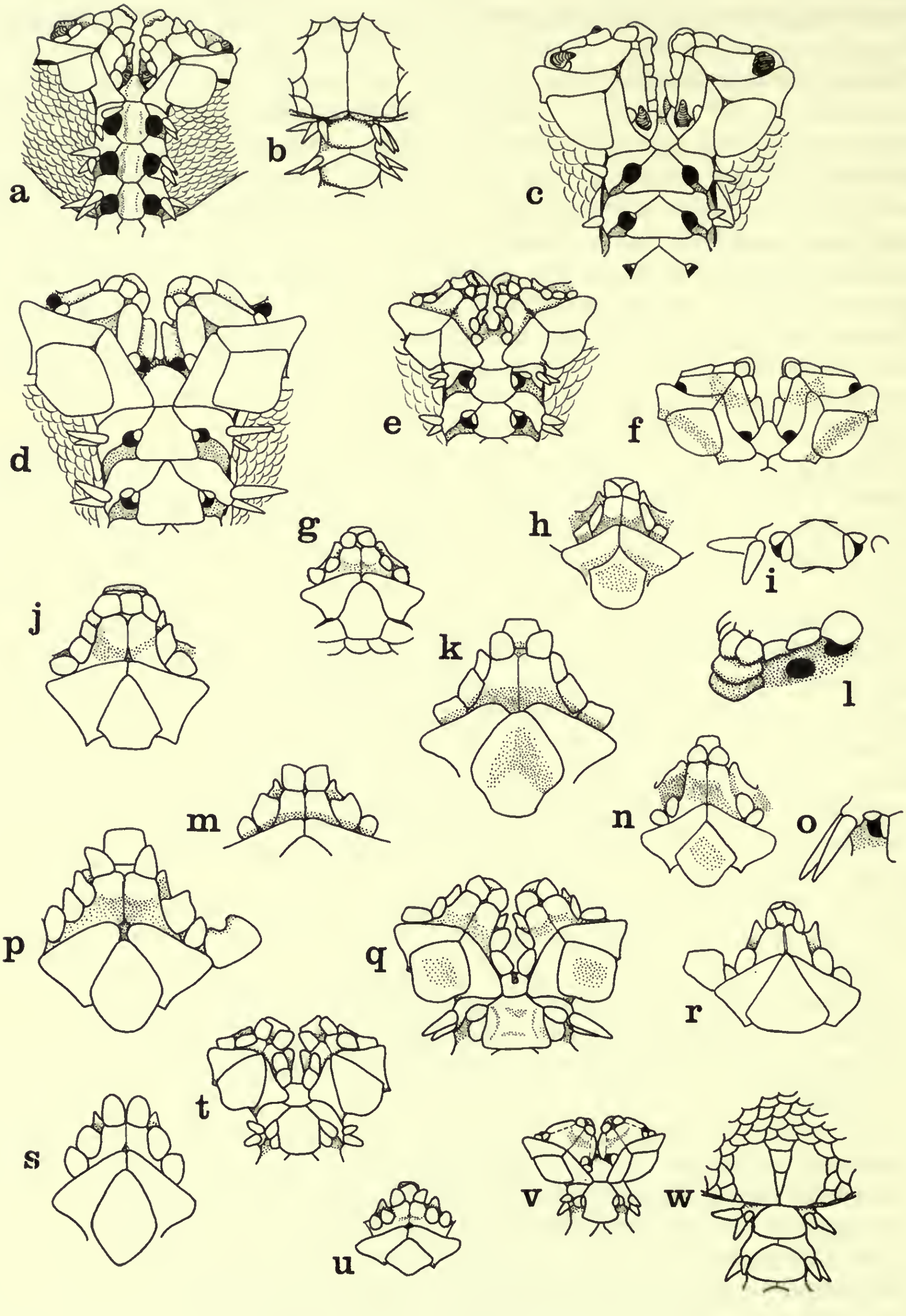
This kind of jaw structure is an incipient modification from that of *Amphioplus* sensu stricto in the direction of *Amphilepis*, since Matsumoto's revision of 1915 isolated in the family Amphilepididae, the relationship of which to the Amphiuridae is discussed further below (p. 70). An even more important modification in my view is that of the arms of *Silax verrilli*. Lyman described the ventral arm plates as swollen but I would call them keeled, though the apex of the keel is blunted. The consecutive dorsal arm plates are separated, even basally, but this condition is shared by a number of other deep-water amphiurids (as well as by *Amphilepis*).

The combination of the keeled arms with the oral structure and the complete absence of tentacle scales even basally in my opinion justifies a generic distinction of *verrilli* from *Amphioplus tumidus* ; I therefore support Fell in this instance in recognizing *Silax* as a valid genus.

Fell (1962) tentatively referred a second species to *Silax*, namely **Amphioplus trepidus** (Koehler, 1904). However, as he comments, this species is not at all Amphiurid-like, not only does the disc merge with the arms dorsally but the radial shields are small and very widely spaced, especially at their distal ends. I have examined the holotype and find that it has a group of *tooth* papillae at the apex of each jaw, numbering six or seven but with two of the more superficial ones arranged as a symmetrical pair, simulating the infradental pair of oral papillae of amphiurids ; usually there is also a single smaller median papilla superficial even to these two. In addition the dorsal-most arm spine is often enlarged on alternate sides of the arm and there are remnants of about eight irregularly-placed spines on the disc, one as much as 0·35 mm. long, the d.d. being only 4 mm. Despite the considerable depth (289 metres) I am certain that the species is referable to the family Ophiocomidae and probably to the genus *Ophiomastix*, which also has disc spines and enlarged uppermost arm spines.

There are, however, a number of other species which show some degree of affinity with *Silax verrilli*. These include the following:

Amphilepis patens Lyman, 1879 W South America ; m,tt,om (fig. 8c)
Ophiomonas protecta (Koehler, 1904) E Indies ; m,oo,m +t (fig. 8d)
Ophiomonas bathybia Djakonov, 1952 W Pacific ; m,oo,m +t
Amphioplus daleus (Lyman, 1879) E Pacific–N and S Atlantic ; m,(m = t)m$\overset{\frown}{n,n}$ (fig. 8l)
Amphioplus patulus (Lyman, 1879) Southern Ocean ; m,(m = t) m$\overset{\frown}{n,n}$ (fig. 8j)
Amphioplus cernuus (Lyman, 1879) N Pacific ; m,(m = t)m$\overset{\frown}{n,n}$
Amphiodia grata (Koehler, 1904) E Indies ; m,(m = t)m,m (fig. 8k)
Amphioplus falcatus Mortensen, 1933a SE Africa ; m,(m = t)m,m
Amphioplus confinis (Koehler, 1904) E Indies ; m,(m = t)m$\overset{\frown}{n,n}$
Amphiura koreae Duncan, 1879 Japan ; m,om,m +t (fig. 8h)
Amphioplus gentilis (Koehler, 1904) E Indies ; m,oM,m +t (fig. 8r)
Amphiodia servata (Koehler, 1904) E Indies ; m,oM,m +t (fig. 8p)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Amphioplus incisus (Lyman, 1883) W Indies ; m,om,m +t (fig. 8q)
Amphiura concolor Lyman, 1879 Japan ; m,om,m +t (fig. 8 g)
Amphiodia caulleryi (Koehler, 1897) Indian Ocean ; m,o$\overset{\frown}{\mathrm{n,n}}$m +t?
Amphiura diomediae Ltk. & Mtsn., 1899 Indo-Pacific ; m,o$\overset{\frown}{\mathrm{n,n}}$m +t (fig. 8n)
Amphiura lunaris Lyman, 1878 W Indies ; m,oo,mm +t (fig. 8v)

Amphichilus cesareus (Koehler, 1905) E Indies ; m,(m = t?)m$\overset{\frown}{\mathrm{n,n}}$
Amphiodia reposita (Koehler, 1905) E Indies ; m,o$\overset{\frown}{\mathrm{N,N}}$m +t (fig. 8m)
Amphioplus conditus (Koehler, 1905) E Indies ; m,om,m +t (fig. 8s)
Amphiodia ochroleuca (Brock, 1888) Indo-Pacific ; m,m,m +t (fig. 8t)
Amphichilus trichoides Matsumoto, 1917 Japan ; m,$\overset{\frown}{\mathrm{n,n}}$m +t
Amphiodia affinis (Studer, 1885) Southern Ocean ; m,omm,o +t (fig. 5j)
Amphiura bidentata H. L. Clark, 1938 Australia ; m,omm, +t (fig. 8u)

The generic names given in the list are those currently in use before 1962 and mainly correspond to the ones given in H. L. Clark's catalogue (1915). The oral formula in some of the species is subject to variation but the version given is believed to be the most common one. The seven species below the dividing line are from shallow water, those above from deep ; only the southern *Amphiodia affinis* ranges from shallow depths to several hundred metres.

A tricuspid lowest tooth similar to that found in the holotype of *S. verrilli*, though a little smaller, occurs on two jaws of the holotype of **Amphilepis patens** (fig. 8c), the two innermost papillae again being offset and not truly infradental, though on

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FIG. 8. a and b. *Silax verrilli* (Lyman), 82.12.23.17, holotype, " Challenger " st. 54, N of Bermuda ; c. *Amphilepis patens* Lyman, 82.12.23.14, holotype, " Challenger " st. 299, off Chile (the tip of one first oral tentacle just shows at top left) ; d. *Ophiomonas protecta* (Koehler), U.S.N.M. 41013, " Albatross " st. 5359, Philippine Is. ; e. *Amphioplus* (*Unioplus*) sp. (*Amphiura concolor* according to Lyman), 82.12.23.455, " Challenger " st. 191, Kei Is. ; f. *Amphilepis norvegica* (Ljungman), 98.5.3.688, Trondhjem Fjord ; g. *Amphiura concolor* Lyman, 82.12.23.107, holotype, " Challenger " st. 195, Banda Sea ; h and i. *Amphiura koreae* Duncan, 80.1.3.4, holotype, Japan Sea (i shows the large tentacle scales on a proximal arm segment) ; j. *Amphioplus* (*Unioplus*) *patulus* (Lyman), 82.12.23.369, holotype, " Challenger " st. 156, Southern Ocean, SW from Australia ; k. *Amphioplus* (*Unioplus*) *gratus* (Koehler), Amsterdam Museum, syntype, " Siboga " st. 211, E Indies ; l. *Amphioplus* (*Unioplus*) *daleus* (Lyman), 82.12.23.370, holotype, " Challenger " st. 325, SW Atlantic, oblique ventral view of superficial part of one side of a jaw ; m. *Amphioplus* (*Unioplus*) *repositus* (Koehler), Amsterdam Museum, syntype, " Siboga " st. 89, E Indies ; n and o. *Amphiura diomediae* Lütken and Mortensen, n. 1948.5.26.56 (pt.), John Murray Expedition st. 54, S Arabian coast, o. 1966.1.20.9, " Albatross " st. 5053, Suruga Gulf, Japan (tentacle scales for comparison with i) ; p. *Amphioplus* (*Unioplus*) *servatus* (Koehler), Amsterdam Museum, holotype, " Siboga " st. 262, (showing the single series of four oral papillae on the left) ; q. *Amphioplus* (*Unioplus*) *incisus* (Lyman), M.C.Z. 1468, holotype, " Blake " st. 161, off Guadeloupe, W Indies ; r. *Amphioplus* (*Unioplus*) *gentilis* (Koehler), Amsterdam Museum, syntype, " Siboga " st. 178, E Indies (see also fig. 11f and g) ; s. *Amphioplus* (*Unioplus*) *conditus* (Koehler), Amsterdam Museum, holotype, " Siboga " st. 89, E Indies ; t. *Amphioplus* (*Amphichilus*) *ochroleucus* (Brock), M.C.Z. 4986, Broome, NW Australia ; u. *Amphiura bidentata* H.L.C., M.C.Z. 4947, holotype, Broome ; v and w. *A. lunaris* Lyman, M.C.Z. 1324, holotype, " Blake " st. 29, Gulf of Mexico.

the three other jaws the teeth are all broadly rounded and the two papillae lie at least partially below the lowest one. As is usual in the genus *Amphilepis*, the apex of the pair of oral plates is less truncated than in most amphiurids, though less so in *patens* than in the type-species, *Amphilepis norvegica* (fig. 8f), and these two innermost papillae are relatively broad and short with their bases at an angle to each other, not in the same plane. Also the oral plates have a superficial flange bearing the first oral tentacle scale. Although in *A. norvegica* this oral tentacle scale is operculiform and extends right to the first ventral arm plate, in *A. patens* it is broken up into two, sometimes three, separate papillae while distally it curves outwards as a rim almost encircling the second oral tentacle, which is superficial in *Amphilepis* ; ventral to the second tentacle, on the edge of the adoral shield, this rim is again rather irregularly divided abradially, usually with a single papilla marked off from it, though Lütken & Mortensen (1899) figure two papillae in this position in their " Albatross " specimen. Lyman failed to record the distal papillae of the holotype.

A very similar oral structure occurs in *Ophiomonas bathybia* with which Djakonov justifiably believes *Amphilepis protecta* to be congeneric. In **Ophiomonas protecta** (fig. 8d) the operculiform first oral tentacle scale is not quite superficial, hence the addition of t at the end of the formula. A similar condition appears to occur in **Amphilepis diastata** Murakami, 1942, which may have the second tentacle even more inset into the oral slit, judging from Murakami's pl. 4, fig. 34 (1963). In 1965 I provisionally referred *diastata* to the synonymy of *Amphiura koreae* (that is sensu Matsumoto, which I now think may be better referred to *diomediae*, see pp. 41–42). It should certainly be included in *Amphiura*, the jaw structure is quite unlike that of *Amphilepis*. Before discussing *Amphiura koreae* there are at least seven species in which the first oral tentacle scale is papilliform and almost superficial, coming more or less into series with the oral papillae ; these include *Amphioplus daleus*, *patulus*, *cernuus*, *cesareus*, *confinis* and *falcatus*, also *Amphiodia grata*, all of which have a basic oral formula of 3m +t like *Silax verrilli*. The first three also approximate to *S. verrilli* in reduction of the tentacle scales, though this was not remarked on by Lyman. In fact the largest of the three holotypes, that of **Amphioplus patulus** (d.d. 14·5 mm.) is the only one to have any tentacle scales beyond the eighth arm segment ; they extend to about the twenty-fifth. The types of **A. daleus** and **cernuus** have d.d. respectively 9 mm. and just under 6 mm. ; the former has the single scales on only the first two segments (with one exception on the third). Some descriptive notes are given below (pp. 44, 45, 58–59 and 62–63) on type-material of the other four species.

A similar 3m +t formula occurs in all the other species in the list but in these the first oral tentacle scale is normally deeper in the oral slit and not in the same superficial plane as the oral papillae. Descriptive remarks for *Amphioplus gentilis*, *Amphiodia ochroleuca*, *reposita* and *servata* are given on pp. 46, 62 and 65–66 and they are also illustrated in fig. 8, as are *Amphioplus incisus* and *conditus*. It can be seen that all of them have a semblance of continuity in the series of oral papillae, the small diastema between the infradental one and the two distal papillae being partially filled by the oral tentacle scale above. This contrasts with species such as *Amphiura lunaris* (fig. 8v, w) and *digitula*, in which the two distal papillae are much more sharply dissociated from the infradental by the long diastema.

A common feature among the deep-water species in the list is irregularity in the symmetry of the infradental papillae. These may be unequal in size (e.g. in the holotype of **Amphiura concolor**, fig. 8 g), or subdivided, usually with three papillae in place of the two (as in the specimen of *Ophiomonas protecta* illustrated here, fig. 8d). Matsumoto (1917) figured this latter condition in what he calls **Amphiura koreae** and it is also found in the holotype of *Amphioplus patulus* (though not in the paratype), causing Matsumoto to refer the latter species to *Amphiactis* which is incorrect, the teeth and the apices of the jaws being broad. The positions of the distal papillae and their relations with the oral tentacle scale are also subject to some variation. Again this has been noted particularly by Matsumoto in the species he calls *Amphiura koreae,* in which the inner of the two distal papillae may be based entirely on the oral plate rather than partially on the adoral shield and sometimes there may be an additional papilla making a total of four or conversely one of the two distal papillae may be lost. Having studied Duncan's holotype of *Amphiura koreae* (fig. 8h, i) I am not altogether convinced that Matsumoto was right in synonymizing with it **Amphiura diomediae** Lütken & Mortensen (1899) (type-locality in the East Pacific) despite the considerable variation also reported by Lütken and Mortensen. Not only is the oral structure of the holotype of *A. koreae* inconsistent with its inclusion in *Amphiura,* the second oral papilla being entirely on the side of the oral plate, but also the oral plates themselves are relatively short, leaving only a very small diastema between the infradental and second papillae, the arm spines are tapering but slightly blunted at the tips and the two tentacle scales (fig. 8i) are distinctly larger than in any of the specimens which I have seen with oral structure like the holotype of *diomediae* (see Lütken and Mortensen's pl. 12 figs. 1, 2), including two paratypes. It also seems to me that in " typical " *diomediae* not only are the arm spines sharper, the tentacle scales smaller and the oral diastemas longer, but also the disc is smoother with flatter scales showing little change of size at the marginal junction, while the other surface plates are also thinner. At least some of the differential characters shown by the holotype of *A. koreae* are shared by Lütken and Mortensen's unnamed variety of *diomediae* (1899, pl. 12, figs. 5–7), namely the shorter oral plates and the more marked size change between dorsal and ventral disc scales. Koehler's specimen (1922, pl. 67, fig. 9) from the Philippines shares at least the second of these characters besides having thicker, and incidently less imbricating, disc scales in the centre. The specimens from the Maldive area (John Murray Expedition station 143) recorded as *diomediae* by H. L. Clark in 1939 also have thickish disc scales, coarser slightly blunted arm spines and the second oral papilla based entirely on the oral plate though the plate itself is relatively longer and the diastema larger than in the holotype of *A. koreae.* The other Murray Expedition specimens, from off the Arabian coast, are more like the holotype of *diomediae* with longer oral plates, sharper spines and smoother discs. I am inclined to think that there are two forms intergrading to some extent but it will need some much larger samples (particularly from Japan) than are available to me at present to investigate this. Unfortunately these two forms together bridge the borderline between *Amphiura* and *Amphioplus,* the holotypes of *diomediae* and *koreae* respectively agreeing in their oral structures with the accepted diagnoses of the two genera—*Amphiura* with a large diastema and one or sometimes two distal oral papillae besides the infradental one, as opposed to *Amphioplus* with a more or less continuous series of four or sometimes three papillae, in each case with the addition of the oral tentacle scale. This emphasizes the close relationship between the two genera. Since none of the other specimens seen by me or figured by others shows either such a small diastema or such large tentacle scales as the holotype of *A. koreae*, I propose to term all of them *Amphiura diomediae*. [As remarked opposite there is also a possibility that *A. diomediae* is conspecific with *Amphiura caulleryi* Koehler, 1897.] The best generic position for specimens with the oral structure of the holotype of *A. koreae* is discussed further on pp. 43-44.

The great geographical range of *Amphiura diomediae* suggests that some of the other deep-sea nominal species in the list above may prove to be synonymous, for instance *Amphioplus daleus, patulus* and *cernuus*, despite the wide separation of their type-localities.

As I mentioned in 1965, the " Challenger " specimens from station 191 (fig. 8e) named *Amphiura concolor* by Lyman are not conspecific with the holotype but are more closely related to *Amphioplus confinis* (Koehler, 1904), differing in having much thinner scales on the disc though the mouth parts are rather similar ; two jaws out of five of the specimen figured have irregular and multiple papillae at the apex but the other three are undeniably amphiurid in form. A similar irregularity often occurs in *Amphiodia affinis*, not only in the apical papillae but also in the more distal ones. The usual arrangement of these is shown in fig. 5j, with the two more distal papillae in series with, though slightly spaced from, the infradental and the third one not quite contacting the adoral shield. However, this is not always the case and there may be a fourth papilla present, also the apical arrangement varies widely, the lowest tooth is often distinctly conical, which provides some justification for Hertz's inclusion (1927) of the species in the genus *Amphiactis*, though the blunt apex of the jaw itself precludes this, while the infradental papillae vary in their spacing and size. An unusual feature is that the oral tentacle scale may be duplicated with two papillae arranged obliquely. [This contrasts with the duplication I have also seen in occasional specimens of species such as *Amphiura diomediae* in which the oral tentacle scale is considerably broadened horizontally and can be split into two parts, only the innermost being at all papilliform.] In fact *Amphiodia affinis* was included in *Amphioplus* by Koehler (1917) but transferred to *Amphiodia* by Mortensen (1936) followed by Madsen (1955). It is a very anomalous species with its very thick disc scales, convex disc, widely-separated radial shields and very short arms tapering abruptly at the tip to a large conical terminal plate and I can understand Studer's reference of a small specimen to the genus *Ophioceramis* (family Ophiuridae) ; only the jaw armament resembles that of amphiurids, especially those from deep water in which the apical structure is similarly somewhat variable. I suspect that a more detailed study of the species will lead to its inclusion in a genus distinct from *Amphioplus* but it certainly cannot be left in *Amphiodia*.

Notes on the type-material of *Amphioplus confinis* and some other interesting 'Siboga' species of Koehler are given on pp. 58 to 66 at the end of the section on

Amphioplus together with a description of a new genus and species based on a specimen in the Museum of Comparative Zoology, Harvard which Lütken & Mortensen (1899) misidentified as *Amphiura* (i.e. *Amphioplus*) *dalea.*

There are two species in the list which are fairly remote from *Silax verrilli* and stand apart from the others by the symmetrical pairing of their two distal oral papillae and their isolation from the infradental one. Firstly **Amphiura lunaris** (fig. 8v, w), of which the holotype (d.d. only 3·5 mm.) has two, sometimes one, distal oral papillae close together on the edge of the adoral shield and an almost superficial flange on each oral plate, the edge of which is indistinctly subdivided in rather the same way as that of *Amphilepis patens* (fig. 8c) ; however, the apex of the jaw is broadly truncated with wide rounded teeth and the infradental papillae are not at all divergent, unlike those of *Amphilepis.* The consecutive dorsal arm plates are not contiguous but this is common to a number of deep-water amphiurids. A better range of material is needed to show the true affinities of the species. Secondly **Amphiura bidentata** (fig. 8u), a shallow-water species, has a rather smaller diastema between the infradental and the two distal oral papillae, both of which are based on the more superficial part of the oral plate, not on the edge of the adoral. These two species are not closely related to each other but it seems best to leave both of them in *Amphiura.* The same may be true of *Amphiura caulleryi* (referred to *Amphiodia* by H. L. Clark in 1915), judging from Koehler's figure which shows a large diastema between the infradental and the pair of distal papillae situated on the adoral " dans l'angle buccal " " recouvrent de chaque côté l'orifice du pore tentaculaire buccal " according to Koehler. In spite of the presence of the first oral tentacle scale on the side of each oral plate, Koehler (1930) follows H. L. Clark in including the species in *Amphiodia.* Until the type-material can be re-examined, the true position of the species cannot be determined though it probably belongs to *Amphiura,* possibly to *Amphioplus,* but certainly not to *Amphiodia.* Koehler's early figures were very diagrammatic and it may be noted that his illustration of *Amphiura reposita* (1905, pl. 4, fig. 13) similarly shows the inner of the two distal papillae as based entirely on the adoral shield whereas in fact it is more often entirely on the oral plate in the holotype and never more than partially in contact with the adoral (see my fig 8m). However, it should be noted that Koehler in 1904 referred *Amphiura caulleryi* to the *Amphioplus* section and simultaneously identified a specimen as *Amphiura diomediae,* referring that species to the *Amphiodia* section. Were it not for this, I would have thought that *caulleryi* and *diomediae* could be synonymous, judging from Koehler's description of 1897 ; the type-locality of *caulleryi* is in the region of Ceylon and *diomediae* has been taken in the Maldive area nearby. A solution of the problem must await a re-examination of the holotype of *A. caulleryi.*

Although the diastema in the papilla series of the holotype of *Amphiura concolor* is hardly more conspicuous than that of species such as *Amphioplus gentilis* and *incisus* and the second papilla arises wholly from the oral plate, I am inclined to leave *concolor* in the genus *Amphiura,* unlike the second specimen referred to the species by Lyman (fig. 8e), which is certainly congeneric with *Amphioplus falcatus.* The problem is even more questionable when it comes to the holotype of *Amphiura koreae.* Strictly speaking, this specimen cannot be regarded as an *Amphiura,* the diastema being so small ; its affinities appear to be all with species such as *Amphioplus daleus*, as far as oral structure goes. However, in view of its other close relationship and even possible identity with *Amphiura diomediae*, it would be irresponsible to refer it to a different genus than *Amphiura*, at least until a more detailed study can be made of large samples from Japanese waters.

It remains to determine the best generic position for the rest of the species in the list above, excluding those just named as better retained in *Amphiura* and the three first species, *Amphilepis patens*, *Ophiomonas bathybia* and *O. protecta* at the top. *Amphiodia* can be ruled out to start with because of the presence of the first oral tentacle scale. This leaves *Unioplus* Fell, *Amphichilus* Matsumoto, *Amphioplus* or *Amphiura*.

The type-species of **Unioplus** is **Amphioplus falcatus** Mortensen, 1933a, from moderately deep water (c. 400 metres) off SE Africa. It has the oral tentacle scale more or less superficial and in series with the true oral papillae, which number three more often than four. A paratype of *A. falcatus* in the British Museum collections shows the considerable variation described by Mortensen in the number and arrangement of the papillae and also has a third infradental papilla between the usual two on three of the five jaws. About half of the papilla series have four papillae plus the oral tentacle scale, the formula being m, (m = t)m, mm but in the rest it is m, (m = t)m,m with minor variations in the precise position of the distal papillae and the vertical alignment of the scale. The dorsal arm plates are barely contiguous but not so markedly separated as in the deep-water species such as *A. daleus* ; also the single tentacle scale extends for almost the entire length of the arm and is not restricted to a few basal segments. The last character distinguishes *falcatus* from *cernuus* and *patulus* which Fell refers to *Unioplus* since both have been described as having a single tentacle scale. *Amphioplus daleus* he omitted since it had been referred by Matsumoto to *Amphichilus*, an interesting taxon intermediate between *Amphiura* and *Amphioplus* (at least as regards oral armament), which was unfortunately not taken into consideration in Fell's revision.

There is some affinity between these three nominal species of Lyman (*daleus*, *cernuus* and *patulus*) and *A. falcatus* but the same cannot be said of most of the other species which Fell has referred to *Unioplus*. At least four of them, *Amphioplus strongyloplax* (H. L. Clark, 1911), *A. thrombodes* (H. L. Clark, 1918) *A. philohelminthius* Ziesenhenne, 1940 and *A. glaucus* (Lyman, 1879) differ from *falcatus* in having bare skin with only scattered scales over part or all of the ventral side of the disc (according to Fell's system thereby justifying further subdivision) and the first two, together with *A. macraspis* (H. L. Clark, 1911), also disagree with the diagnosis of *Unioplus* in having two tentacle scales on some of the proximal pores rather than one. They differ too in having the oral tentacle scale higher in the slit and usually four oral papillae (though in *strongyloplax* and *macraspis* the fourth or outermost rather than the second papilla may be lacking.) Of the other species referred to *Unioplus*, **Amphioplus formatus** (Koehler, 1905) (fig. 11a, and see pp. 61–62) is probably not an Amphiurid at all ; the holotype and only recorded specimen has very narrow elongated teeth and the two innermost papillae of each jaw are offset to the sides of the lowest tooth, though they each form a straight series of four with the other oral papillae, the distalmost of which is the broadest ; the formula is $\overset{\frown}{\mathrm{n,n}}$mm,M—t. The oral shields are relatively very small and almost circular and the adorals are comparatively large and very broadly contiguous inwardly. Tentacle scales are lacking altogether on the first four to seven segments. The arms are only about three times the disc diameter and the arm spines are extremely long, even exceeding the width of the arm. The holotype of **Amphioplus capax** (Koehler, 1905) has d.d. only 1·5 mm. and was very decalcified when I saw it recently ; most of its characters are juvenile ones but Koehler figures four oral papillae in a straight row and unusually elongated oral shields. The type of **Amphioplus aciculatus** Mortensen, 1936 is also small, d.d. 2 mm. ; its oral formula is m,om,mm+t and the inner one of the two distal papillae is spiniform. The holotype of **Amphioplus dispar** (Koehler, 1897) also has the second from outermost papilla spiniform but otherwise shows no particular resemblance to *aciculatus*.

With the possible exception of *A. daleus* and its two allies and *A. falcatus*, there appears to me to be no particular affinity between any of these species and I do not consider that *Unioplus* can be maintained on the basis of the single tentacle scale alone. However, it may be worth redefining in terms of the oral structure for some of the species in the list on pp. 37–39. Even so, the oral structure is liable to confusion with that of **Amphichilus**, which also has only three oral papillae, though in the type-species, **Amphichilus trichoides** Matsumoto, 1917, the tentacle scale is distinctly higher in the oral slit and the formula is better expressed as $\mathrm{m,o}\overset{\frown}{\mathrm{n,n}}\mathrm{m,+t}$ than as $\mathrm{m,(m = t)}\overset{\frown}{\mathrm{n,n}}\mathrm{m}$, as in *Amphioplus falcatus*. The radial shields of *Amphichilus trichoides* are almost fully contiguous, unlike those of most of the other species under consideration ; Matsumoto included this in his generic diagnosis. He also referred *Amphioplus daleus* (Lyman, 1879) as well as *A. intermedius* (Koehler, 1905) to *Amphichilus*. I do not consider *A. daleus* is closely related to *Amphichilus trichoides*; apart from being a deep-sea species it has separated or barely contiguous radial shields, non-contiguous dorsal arm plates, no tentacle scales (except a single one on a few of the basal pores) and irregular apical oral papillae on some jaws. In the holotype of **Amphioplus intermedius** I found the second papilla to be perfectly in series with the other three, the four oral papillae closing the slit so well that it is impossible to tell without mutilation if the oral tentacle scale is also present behind the papillae ; the general appearance of the jaws agrees well with that of *Amphioplus impressus* (Ljungman, 1867b), unlike *Amphichilus trichoides*.

Koehler (1930) has referred **Amphioplus cesareus** (Koehler, 1905) to *Amphichilus* with some justification ; it has almost fully contiguous radial shields and comes from relatively shallow water, usually 5–100 metres ; in one of the two syntypes in the Amsterdam Museum the second oral papilla is slightly inset in some series and with its conical rather than square shape is clearly homologous with the oral tentacle scale which is otherwise missing. However, after comparison of specimens named both *Amphiura cesarea* (or *Amphichilus cesareus*) and *Amphioplus impressus* by Koehler at different times (see pp. 63–64) with the same author's description and figures of the type-material of *A. impressus*, I have come to the conclusion that *cesarea* is a synonym of *impressus*. The normal position of the second oral papilla in the species is superficial (fig. 9m) and, like *A. intermedius*, I do not think that it can be referred to *Amphichilus*. These two species differ most obviously from one another in the much finer disc scaling of *intermedius* ; together they form a link between *Amphichilus* and *Amphioplus* sensu stricto as well as between the latter and *Amphipholis*, from which only the presence of a fourth oral papilla distinguishes them, the outermost papilla approximating to an opercular form. However, I believe that **Amphiodia ochroleuca** (Brock, 1888) (fig. 8t) can be referred to *Amphichilus* ; it is another shallow-water Indo-West Pacific species and cannot be left in *Amphiodia* since it has the first oral tentacle scale present ; this scale is distinctly higher than the oral papillae, of which the two outer ones are fairly broad and rectangular. Like *A. trichoides* the radial shields are contiguous, though in some specimens only for their distal halves.

In contrast, all the other species under consideration, like *Amphioplus falcatus*, have the radial shields only contiguous by their distal adradial corners or else separated altogether. Apart from the single antiboreal species *Amphiodia affinis* (Studer, 1885), which ranges in depth from shallow-water to several hundred metres, and with the exception of *Amphiodia reposita* (Koehler, 1905) and *Amphioplus conditus* (Koehler, 1905), all these are from deep-water (400+ metres, many of them 1000+ metres). [By coincidence, the type- and only recorded specimens of the two latter species were labelled as coming from " Siboga " station 89, the depth of which was only 11 metres ; it seems suspicious that they have not since been collected

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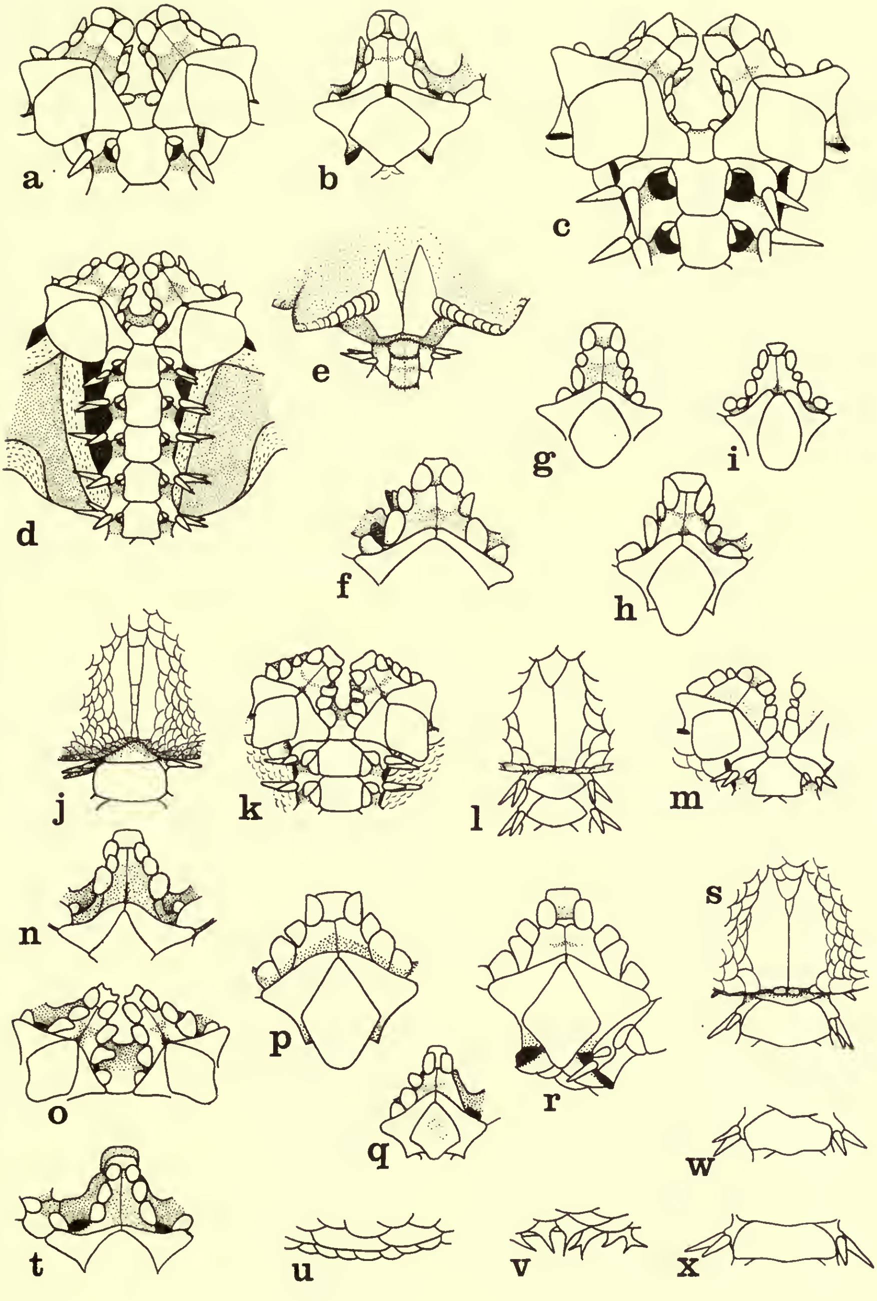
FIG. 9. *Amphioplus* spp. (except t). a. *A. tumidus* (Lyman), M.C.Z. 1476, holotype, " Blake " st. 47, Gulf of Mexico ; b. *A. strongyloplax* (H. L. Clark), U.S.N.M. 25615, holotype, off Washington ; c. *A. cyrtacanthus* H. L. Clark, M.C.Z. 1489, holotype, Philippine Is. ; d and e. *A. coniortodes* H. L. Clark, M.C.Z. 4217, holotype, Key West, Florida, the disc shrunk away from the arm base ; f–i. *A. abditus* (Verrill), showing the exceptional variation in the oral papillae and oral tentacle scale, f. B.M. 90.8.23.43, Martha's Vineyard (the oral shield shown is the madreporite), an oral tentacle scale occurs on one side in addition to the second oral papilla (the two oral tentacles are also shown on this side), g. U.S.N.M. 18007, holotype of *A. macilentus* (Verrill), a synonym, off New England, with five superficial papillae one side and four the other, h. M.C.Z. 1456, Noank, Connecticut, with no second papilla but the oral tentacle scale more or less superficial, i. M.C.Z. 4842, Charleston, South Carolina, with superficial second papilla presumably representing the oral tentacle scale though rounded in shape and with an interstitial papilla between third and fourth on one side (and in five other series) ; j and k. *A. stenaspis* H. L. Clark, M.C.Z. 4990, holotype, near Darwin ; l and m. *A. impressus* (Ljungman), U.S.N.M. 41171, " Albatross " st. 5371, Philippine Is. ; n. *A. archeri* A.M. Clark, B.M. 1956.5.23.1, paratype, Ghana ; o. *A. cinctus* (Koehler), B.M. 1956.5.23.21, off Accra, Ghana, the two middle papillae of the left-hand series reflexed ; p and q. *A.* (*Lymanella*) *hastatus* (Ljungman), p. Amsterdam Museum, " Siboga " st. 167, W of New Guinea, " absolument conforme à l'exemplaire type de Ljungman " (Koehler), q. B.M. 1948.5.26.92, John Murray Expedition st. 89, northern Arabian Sea (d.d. only 3·5 mm.), the three distal oral papillae removed on one side to show the rudimentary oral tentacle scale ; r. *A.* (*Lymanella*) *megapomus* H. L. Clark, U.S.N.M. 25633, holotype, " Albatross " st. 4964, Japan ; s. *A.* (*Lymanella*) *laevis* (Lyman), M.C.Z. 5590, syntype of *A. praestans* (Koehler), "Siboga " st. 11, Java Sea ; t. *Paracrocnida persica* Mortensen, B.M. 1964.7.17.26, Eilat, Gulf of Akaba ; u. *Amphioplus* (*Lymanella*) *depressus* (Ljungman), Amsterdam Museum, " Siboga " st. 51, Molo Strait, E Indies (named *Amphiura relicta* by Koehler, 1905), edge of disc from above ; v. *A.* (*Lymanella*) *spinulosus* (Koehler), Amsterdam Museum, paratype, " Siboga " st. 319 (not in published report but added MS to Amsterdam Museum copy), Java Sea, edge of disc from below ; w. *A.* (*Lymanella*) *laevis* (Lyman, M.C.Z., holotype, third dorsal arm plate (from drawing by Miss A. Schoener) ; x. *A.* (*Lymanella*) *megapomus* H. L. Clark, holotype (as above).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if this was true.] It is possible therefore to redefine *Unioplus* in terms of the 3m+t formula (often with t = m) coupled with the divergent or separated radial shields contrasting with those of *Amphichilus*. Also most of the species to be included in *Unioplus* show some irregularity in the armament of the apex of each jaw and the consecutive dorsal arm plates are barely contiguous or even separated.

Neither *Unioplus* nor *Amphichilus* seems to me to be sufficiently distinct for recognition at the generic level. There is clearly considerable variation in the oral structure, not only in the species already discussed but also in others such as *Amphioplus abditus* (Verrill, 1871) (see fig. 9f–i) and *Amphioplus timsae* Mortensen, 1926. In addition, as I remarked in 1965, the relationship between *Amphiura* and *Amphioplus* is very close, as exemplified by the *Amphiura koreae–diomediae* problem detailed above, as well as by some geographically coincident species such as the Japanese *Amphiura digitula* (H. L. Clark, 1911)—an *Amphiura* with two distal oral papillae—and *Amphioplus ancistrotus* (H. L. Clark, 1911). Accordingly I think it best to reduce both *Unioplus* and *Amphichilus* to the rank of subgenera of *Amphioplus*. This accords with Verrill's original diagnosis of *Amphioplus* as having four or five oral papillae in each series since he included the oral tentacle scale in his papilla count.

AMPHIOPLUS subgenus ***UNIOPLUS*** Fell, re-defined

Amphioplus (part) : Mortensen, 1933a, and others.
Unioplus Fell, 1962a : 16. Type-species : *Amphioplus falcatus* Mortensen, 1933a.

DIAGNOSIS. A subgenus of *Amphioplus* including species with the second oral papilla normally suppressed but the first oral tentacle scale often more or less superficial and taking a place in the papilla series after the infradental papilla, so that the oral formula usually approximates to m, (m=t)m,m or m,om,m+t ; the infradental papillae and lowest tooth usually rather variable in size, shape and arrangement, sometimes asymmetrical ; the two radial shields of each pair either just touching by their distal adradial corners or else completely separated by the scales ; successive dorsal arm plates barely if at all contiguous ; tentacle scales numbering one or two, sometimes none except on the basal pores.

The following nominal species are referable to *Unioplus*[1] :

Amphiura cernua Lyman, 1879 : 28. N Pacific, E from Japan.
Amphiura dalea Lyman, 1879 : 27. SW Atlantic.
Amphiura patula Lyman, 1879 : 31. Southern Ocean, SW from Australia.
Amphiura incisa Lyman, 1883 : 250. West Indies.
Amphiura affinis Studer, 1885 : 162. South Georgia.
?*Amphiura caulleryi* Koehler, 1897 : 330. Ceylon area.
Amphiura confinis Koehler, 1904 : 89. East Indies.
Amphiura gentilis Koehler, 1904 : 86. East Indies.
Amphiura grata Koehler, 1904 : 85. East Indies.
Amphiura servata Koehler, 1904 : 84. East Indies.

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[1] In original combination, chronological order and with type-localities.

Amphiura condita Koehler, 1905 : 46. East Indies.
Amphiura reposita Koehler, 1905 : 40. East Indies.
Amphiura falcatus Mortensen, 1933a : 365. SE Africa. Type-species.

Of all these, only *Amphioplus cernuus* and *patulus* were included in *Unioplus* by Fell, besides the type-species.

AMPHIOPLUS subgenus *AMPHICHILUS* Matsumoto

Amphichilus Matsumoto, 1917 : 175. Type-species : *Amphichilus trichoides* Matsumoto, 1917.

DIAGNOSIS. A subgenus of *Amphioplus* including species with the second oral papilla suppressed and the first oral tentacle scale inset, so that the oral formula is m,m,m+t or m,n͡,nm+t ; armament of jaws normally symmetrical ; the two radial shields of each pair contiguous for at least the distal half of their length, often more ; dorsal arm plates contiguous, at least medially ; two tentacle scales in the two species now included.

The following are referable to *Amphichilus* :

Amphiura ochroleuca Brock, 1888 : 484. East Indies.
Amphichilus trichoides Matsumoto, 1917 : 175. Japan. Type-species.

AMPHIOPLUS sensu extenso (cont.)

As for **Ailsaria**, apart from the type-species, **Amphioplus echinulatus** Mortensen, 1940, Fell refers to it *Amphioplus archeri* A. M. Clark, 1955, *A. coniortodes* (H. L. Clark, 1918) and *A. personatus* (Koehler, 1905). Of these, **Amphioplus archeri** is not at all closely related to *echinulatus* ; its radial shields are short, wide and fully contiguous, rather than elongated and more than half separated proximally and the oral shields too are quite a different shape ; the oral formula (from Mortensen's figure) is m,on͡,nmm+t in *A. echinulatus* but normally m,mm,on͡,n—t in *A. archeri* (figs. 1i, 9n), there being no oral tentacle scale on most jaws and a distal rather than proximal gap in the sequence of papillae ; the arm structure is also very different in *A. archeri*. In **Amphioplus coniortodes**(fig. 9d, e) the dorsal disc scaling is fine and indistinct, the oral shields are triangular with no distal lobe, the oral formula is m,omm,om+t or m,(m = t)mm,om, the oral tentacle scale being more or less in series with the oral papillae while the arm spines are simple at the tip, numbering only three rather than five with hooked tips, as in *echinulatus*, or eight proximally as in *A. archeri*. In the holotype of **Amphioplus personatus,** (see also pp. 64–65) the oral formula is m,omn͡,nn͡,n+t, the distalmost papilla being based partly on the first ventral arm plate ; with its rather similar oral formula, divergent radial shields, five arm spines and spearhead-shaped oral shields with a distal lobe (though this is a little wider than it appears in Koehler's figure) *A. personatus* may prove to be closely related to *A. echinulatus* (both of them are from the Indo-West Pacific) but it does not agree with the two Atlantic species, *archeri* and *coniortodes*. Because of its oral structure, I think *A. archeri* is more closely related to **Amphioplus cinctus** (Koehler, 1914) (fig. 9o) which has the disc fully scaled below, while *Amphioplus echinulatus* shows a parallel affinity for the fully-scaled *A. timsae* Mortensen, 1926.

These observations lead me to the conclusion that the following is not a valid taxon of the genus-group and should be referred to the synonymy of *Amphioplus* Verrill, 1899 :

Ailsaria Fell, (type-species *Amphioplus echinulatus* Mortensen, 1940).

As I noted in 1965, among the many species of *Amphioplus* with two tentacle scales, a natural group exists which differs from the type-species, *A. tumidus* (Lyman, 1878) (fig. 9a) in having the four oral papillae in a continuous row, their free edges forming a straight line so that they are capable of closing the oral slit almost completely, the third papilla being distinctly enlarged, often truncated conical in shape, while the oral tentacle scale is rudimentary and concealed behind the papillae, if present at all ; at the same time the radial shields are contiguous for more than half their length, there are only three arm spines and the two tentacle scales are large or very large, also there is often some specialization of the disc scales in the marginal region at the line of junction of the dorsal and ventral scales.

The most frequently recorded species of this group are probably *Amphioplus depressus*, *integer* and *hastatus* (fig. 9p, q), all described (as *Amphipholis*) by Ljungman, 1867b, also *Amphioplus laevis* (Lyman, 1874), *relictus* (Koehler, 1898) and *japonicus* (Matsumoto, 1915).

H. L. Clark (1918) first referred **japonicus** to the genus *Amphioplus*, protesting that it has no true articulated marginal papillae and four rather than three oral papillae, unlike *Ophiophragmus wurdemanni* Lyman, the West Indian type-species of *Ophiophragmus*, which up to that time had never been properly figured. However Matsumoto (1941) persisted in including *japonicus* in *Ophiophragmus*, Koehler (1930) and Murakami (1943 and 1944) following the same practice, though in 1963 Murakami uses the generic name *Amphioplus* ; Matsumoto's grounds for this were that *japonicus* is distinguished from *Amphioplus* by the absence of the first oral tentacle scale. I have seen a number of specimens of *japonicus* but have not observed this scale in any of them; however, I have found it, at least in rudimentary form, on some oral plates of certain individuals of *Amphioplus hastatus*, *A. laevis* and particularly *A. integer*, all of which but especially the first are closely related to *japonicus*. The marginal " fence " on the disc of *A. japonicus* consists of the enlarged scales of the outermost dorsal row bordered by the up-turned scales of the uppermost ventral row which in young specimens Matsumoto found to be sufficiently prominent to form a " hem-like row of denticles " so that the disc edge is serrated. Comparable modifications of the marginal scales have also been recorded in *A. furcatus* (Mortensen, 1933a), in *A. hastatus* by Mortensen, 1940, in *A. gibbosus* (Ljungman, 1867b) and in *A. affinis* (Duncan, 1887) ; also in *A. relictus* (by Koehler in 1922(a) though I believe that he confused *relictus* and *japonicus* in this work), while in *A. spinulosus* (Koehler, 1904) (fig. 9v) even greater modification occurs. Not all individuals of *japonicus* show the marginal " fence " or flange and Mortensen (1940) notes that marginal thorns may be present or absent in *hastatus* in the Persian Gulf, so their occurrence is not diagnostic.

In amphiurids such as *Amphioplus* with numerous oral papillae there is often considerable variation in the arrangement of the papillae and their relationship with the first oral tentacle scale. It should not be forgotten that the two distalmost oral papillae of *Amphioplus* are homologous with the scales of the second oral tentacle, as indeed Verrill (1899) termed than in his diagnosis of *Amphioplus*. It is then more understandable that the *first* oral tentacle scale can be transformed into an oral papilla by shifting to a superficial position, as already described in species such as *A. falcatus* or alternatively more or less suppressed at the expense of the oral papillae as in the group of species now under discussion.

In fact a straight row of four oral papillae with no visible oral tentacle scale is not restricted to the species of the *hastatus*-group, being shared notably by *Amphioplus impressus* (Ljungman, 1867b) (fig. 9m), *intermedius* (Koehler, 1905) and *aurensis* A. M. Clark, 1955. These also have contiguous radial shields and only three arm spines but are distinguished from the *hastatus*-group by the smaller size of the two tentacle scales and the enlarged fourth rather than third oral papilla.

In **A. stenaspis** H. L. Clark, 1938 (fig. 9j, k) and *A. iuxtus* Murakami, 1943, also the oral papillae are in a straight row and at the same time the tentacle scales are very large, but both species have more than three arm spines proximally and their radial shields are separated or only contiguous for less than half their lengths, also in *A. stenaspis* at least the oral tentacle scale is present and visible above the oral papillae.

Amphioplus causatus and *exsecratus* (Koehler, 1905), as well as *A. cinctus* (Koehler, 1914) and *ailsaclarki* Cherbonnier, 1957 (if the last two are distinct) resemble *hastatus* in the oral structure even to the extent of having the third oral papilla the largest ; they also have fairly large tentacle scales and, with the possible exception of *exsecratus*, the radial shields largely contiguous (though for only about half their length in *causatus*). However, *causatus* has four arm spines proximally and the others often have five ; even so it might be better to ally *cinctus* (and *ailsaclarki*) with the *hastatus*-group by setting aside the distinction of arm spine number ; although most specimens studied appear to have the oral papillae in a concave row, this is largely an illusion caused by the extension of the second oral tentacle and the erection of the third and fourth papillae to the vertical position.

There are of course several other species of *Amphioplus* with only three arm spines or with two more or less enlarged tentacle scales, sometimes both together.

Clearly none of these characters is restricted to the species of the *hastatus*-group, although they combine to distinguish it. Accordingly the limits are not sharply defined and I consider that the group merits only the rank of a subgenus.

AMPHIOPLUS subgenus *LYMANELLA* nov.

TYPE-SPECIES. *Amphipholis hastata* Ljungman, 1867b. [See Koehler, 1927a, pl. 3, figs. 2 and 3 for photographs of the holotype.]

DIAGNOSIS. A subgenus of *Amphioplus* in which the four oral papillae are arranged in a continuous row with their free edges (when aligned horizontally) forming a straight line, so that they can almost completely close the oral slit, the third papilla being more or less distinctly enlarged so that the formula is m,m$\overset{\frown}{\text{N,N}}$m +/—t ;[1] the radial shields are contiguous for over half their lengths ; the two tentacle scales are large or very large, more or less completely covering the corresponding pores and the arm spines number not more than three. In some of the species the uppermost ventral row of disc scales (which usually comes just above the margin in preserved specimens) may project in a flange or else have small thorny prolongations of the scales ; rarely (*A. spinulosus*) the thorns are larger, rather like those of the subgenus *Amphispina* of *Amphiodia* but are still extensions of the scales and not articulated.

The following nominal species are referable to *Lymanella*[2] :

Amphipholis hastata Ljungman, 1867b : 313. Mozambique.
Amphipholis depressa Ljungman, 1867b : 312. Java–Singapore.
Amphipholis integra Ljungman, 1867b : 313. Port Natal.
Ophiophragmus gibbosus Ljungman, 1867b : 316. Port Natal.
Amphipholis andreae Lütken, 1872 : 106. Java.
Amphiura laevis Lyman, 1874 : 229. Philippine Is.
Amphiura congensis Studer, 1882 : 19. Congo, West Africa.
Ophiophragmus affinis Duncan, 1887 : 89. Mergui Archipelago, Burma.
Amphiura relicta Koehler, 1898 : 69. Bay of Bengal.
Amphiura (*Amphioplus*) *spinulosa* Koehler, 1904 : 92. Lesser Sunda Is.
Amphiura (*Amphioplus*) *praestans* Koehler, 1905 : 52. Lesser Sunda Is.
Amphioplus megapomus H. L. Clark, 1911 : 170. Southern Japan.
Ophiophragmus japonicus Matsumoto, 1915 : 70, with var. parvus Matsumoto, 1941 : 334. Japan.
Amphioplus bocki Koehler, 1927b : 6. Fiji.
Amphioplus potens Koehler, 1930 : 107. Kei Is.
Amphioplus furcatus Mortensen, 1933a : 370. Natal.
Amphioplus caelatus Ely, 1942 : 39. Hawaiian Is.
Amphioplus miyadii Murakami, 1943 : 227. Southern Japan.

Of these eighteen names, several have already been relegated to the synonymy of others and I think that when a proper appreciation is reached of the extent of variation, especially of the disc in relation to growth and regeneration, the total number of species recognized will be less than half that number.

Mortensen (1940) considers that *A. furcatus* is a synonym of *A. hastatus*, which he found in abundance in the Persian Gulf, although the type-material of *furcatus* appears to me to have relatively finer and more numerous disc scales than is usual in *hastatus* of the same size.

At the same time Mortensen notes that **Amphioplus bocki** could be a synonym of **A. laevis**. However, since Lyman published only very poor figures of the

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[1] In preserved specimens the third oral papilla particularly may be found projecting outwards so that the small, V-shaped gap between its tip and that of the fourth papilla, through which the second oral tentacle may be seen, is considerably widened. This is the case in the holotype of *A. bocki* Koehler, 1927b for instance.

[2] With original combinations, in chronological order and with type-localities.

holotype of *A. laevis*, this is uncertain. Unfortunately I omitted to study the holotype when visiting the Museum of Comparative Zoology, Harvard, but Miss Amy Schoener tells me that it is in poor condition with only a few damaged basal segments of the arms left attached to the disc. Her drawing of an arm base (fig. 9w) shows rather irregular dorsal arm plates with some suggestion of a median angle in their distal sides but with the broadest part of the plate towards the proximal end which is unusual. The specimen figures by Mortensen (1940) under the name of *laevis* has distinct median distal angles to the dorsal arm plates but the broadest part of each plate is near the distal end. This is just the shape figured by Koehler from a syntype of **Amphioplus praestans** and found also in another syntype in the Harvard Museum (fig. 9s), although some of the smaller " Siboga " specimens in the Amsterdam Museum have little sign of a median distal angle to these plates. In some ways it might be best to reject the name *laevis* on the grounds of the almost unrecognizable condition of the holotype but the name has been widely used in recent years for the species figured by Mortensen. Koehler (1905) referred two small " Siboga " specimens (d.d. c. 5 mm.) to *laevis* at the same time that he described *praestans* and these two have particularly narrow radial shields, length : breadth = 3·5–3·75 : 1 (4 : 1 in the holotype according to Lyman), while their oral shields are relatively broad, though still longer than broad. Nevertheless I do not think that either is beyond the range of variation of a single species, nor is the slight difference in the shape of the dorsal arm plates compared with the holotype significant. There are specimens in the British Museum collections from the Red Sea, New Guinea and the Solomon Islands which agree with the type-material of *praestans* and at the same time with Lyman's description of *laevis* in having the disc flat and usually thin and more or less sharp at the edge, the scales and plates thin and the spines slender. The distinctive light line along the arms mentioned by Lyman is an illusion caused by the thinness and semitransparency of the arm plates, allowing the mid-line of the vertebrae to show through. Unfortunately most of the specimens studied have the arms more or less badly broken, except for some from the Solomon Islands in which the arm length is about ten times the d.d. This compares with a proportion of 13–14 : 1 for the type-material of *A. bocki*. However, I am inclined to think that Mortensen may be right in referring *bocki* to the synonymy of *laevis*. Even so, it should be noted that Koehler describes the arm spines of *bocki* as blunt-tipped whereas in all the specimens I regard as referable to *A. laevis* the slender spines are more or less sharp.

Matsumoto (1941) thinks that **Amphioplus megapomus** is allied to his variety parvus of *japonicus* but, as noted in 1965, I doubt this since the discless holotype of *megapomus* (fig. 9x) is another specimen with a median distal angle on each dorsal arm plate, differing in this from *japonicus*. H. L. Clark in 1915 recorded four smaller Japanese specimens as *megapomus*, noting that their radial shields are relatively short. However, he also notes that their arm plates show some differences from those of the types and it is possible that they were not conspecific in view of the number of other nominal species of *Lymanella* recorded from Japan. If the identification was correct and the radial shields are short in *megapomus* then it is very close to *A. andreae*, but if long then the affinity is with *laevis* again, or with **Amphioplus miyadii,** if that is itself distinct from *laevis*.

H. L. Clark (1918) and Koehler (1922a) both note that **Amphioplus affinis** (Duncan) is a homonym of *A. affinis* (Studer, 1885) (though Mortensen in 1936 and Madsen in 1955 put *affinis* Studer in *Amphiodia*) and that Duncan's material was probably conspecific with *A. relictus*. However, the Kagoshima specimens figured by Koehler in 1922(a) (pl. 71, figs. 7 and 8) named by him **Amphioplus relictus** appear to be conspecific with *A. japonicus* of which Kagoshima is the type-locality. Koehler's earlier specimens from the Indian Ocean which he named *relictus* at least may be distinguishable from *japonicus* by the longer distal lobes of their oral shields (though the shape of these is variable in many of the species of *Lymanella*) but his figures are so diagrammatic that this is not certain. In 1930 he recorded *Ophiophragmus japonicus* from the Gulf of Siam and Amboina, thus extending the range well beyond Japan, though simultaneously he recorded other specimens from these same areas as *Amphioplus relictus*. H. L. Clark (1946) refers *relictus* to the synonymy of *depressus*, which seems to me well justified. I am even doubtful whether *depressus* and *japonicus* can be distinguished from *hastatus*. All of them have relatively broad radial shields, opaque scales and plates, no marked median distal angle to the dorsal arm plates and often more or less specialized marginal scales (fig. 9u). The distinction of **Amphioplus hastatus** from the others by its prominent primary rosette is not reliable because of the likelihood of loss and regeneration, in which case the rosette is probably not reformed. Mortensen (1940) records a number of discless specimens and assumes that the loss was incurred during capture since there is no sign of regeneration. However, I suggest that natural loss may occur during the breeding season when the disc is liable to be distended but this remains to be investigated. The considerable length of the distal lobe of the oral shields (fig. 9p) is also supposed to distinguish *hastatus*. Certainly all 21 Japanese specimens which I referred to *japonicus* in 1965, have a very short distal lobe, more of a convex side, however, a very similar form of shield occurs in a specimen of *hastatus* (fig. 9q) from the northern Arabian Sea (John Murray Expedition) as well as in Koehler's 1905 figure of *hastatus*. Unfortunately Koehler did not include **Amphioplus depressus** among those of Ljungman's types of which he gave photographs in 1927(a), though in 1930 he illustrates a specimen with d.d. 5 mm. which he says is very like the holotype. The scales of this specimen are thick and stand out in relief and the central disc scales though large do not form a proper rosette ; it also has very long distal lobes to the oral shields, although Ljungman described those of the type as having " angulo externo parum producto ". It does not seem markedly different from some of the specimens which I have seen attributed to *hastatus*.

Lyman (1882) referred two lots of " Challenger " specimens to *A. depressus*. The single discless specimen from Japan is almost certainly conspecific with *A. megapomus* since it has median distal angles to the dorsal arm plates. The other two are from Fiji, one having the disc intact and measuring 9·5 mm. in diameter. The primary rosette is just distinct though the radial plates are very little larger than the scales around them ; on a line between the radial shields across each interradius there are seven to nine scales. The radial shields are fairly wide and almost triangular in shape with length : breadth 2·3 : 1 and length : disc radius 1 : 2·7. The uppermost row of ventral disc scales form a projecting flange. The dorsal arm plates are extremely wide (as might be expected at this large size) and the dorsal side of the arms is very convex, though when viewed immediately from above the distal edges of the plates appear straight. The oral shields are narrow spearhead-shaped with the distal lobe only a little shorter than the proximal angle and not very constricted. There is no sign of an oral tentacle scale in either specimen. Three other specimens in the British Museum collections can also be referred to *A. depressus* ; these are from Madras in 9 metres depth and all have d.d. c. 5 mm. The primary rosette can just be distinguished in two of them and two have a slight marginal flange. The radial shields are relatively larger than in the Fiji specimen (in conjunction with the smaller total size), the ratio of length : disc radius being 1 : 2·5 in one specimen and 1 : 2·2 in the other two. The dorsal arm plates are convex distally but this curve is truncated medially to some extent.

The largest Murray specimen of *A. hastatus* has d.d. 5 mm. It also has relatively large radial shields with length : disc radius 1 : 2·1 and length : breadth c. 1·8 : 1. The primary rosette is quite distinct, there are about seven scales between the radial shields interradially and the disc has a sharp margin but no modification of the scales into a fringe of spiniform processes as Mortensen describes for some specimens from the Persian Gulf (1940). A rudimentary oral tentacle scale is present though normally concealed behind the oral papillae and the oral shields have only a short distal lobe. [A specimen from the Red Sea recorded as *hastatus* by Burfield (1924) with d.d. only 3·2 mm. has relatively longer radial shields, length : breadth 2·5–2·8 : 1 and the scales are much smaller with 11–13 in a line between neighbouring radial shields interradially. Also the dorsal arm plates have a slight median distal angle. Accordingly I have re-identified Burfield's specimens as *A.* (*Lymanella*) *laevis*.]

Some of the other nominal species listed are also very closely related, for instance **Amphioplus integer** and **caelatus**, and need further investigation of their ranges of variation. Although it has often been noted that most of the species are liable to lose their discs very easily, little account has been taken of the consequences of regeneration on the characters shown by the disc, such as the distinctness of the primary rosette, the proportions of the radial shields, the size of the scales and the modification, if any, of the marginal scales. While regeneration is in process the newly formed radial shields undergo a marked change, starting as short wide separate plates but becoming longer and more contiguous as the disc grows to the original size. Mortensen (1933a) illustrates a regenerating specimen of *A. integer* showing an early stage in the regrowth of the radial shields and Koehler's figure 3, pl. 18 (1930) of the type and only specimen of **Amphioplus potens**, which is clearly in process of regeneration but at a rather later stage, shows the shields in contact but barely longer than wide and the whole disc still diminutive. I believe that *potens* will prove to be a synonym of either *A. andreae* (if its radial shields were originally short with a length : breadth ratio of c. 2 : 1) or *A. laevis* (if the ratio was about 3 : 1). There is of course some variation in the proportions of the fully-grown radial shields ; as noted in 1965, those of 21 specimens of *A. japonicus* have the length : breadth ratio ranging from 1·75 to 2·55 : 1, averaging 2·1 : 1. In 15 specimens of *A. integer* (the only other sample of any size available) the variation is greater, from 2·3 to 3·7 : 1, averaging 2·8 : 1.

It remains to give a diagnosis of the genus *Amphioplus* as reconstituted, as well as of the subgenus *Amphioplus*, excluding the species now referred to *Unioplus*, *Amphichilus* and *Lymanella* ; also to construct a diagram illustrating the possible relationships between these taxa and some other amphiurids.

Genus ***AMPHIOPLUS*** Verrill

Diagnosis. A genus of Amphiuridae with three or, more usually, four oral papillae forming a fairly continuous series on each half of the jaw, the consecutive ones either contiguous or else separated by relatively small spaces much less conspicuous than the large diastema of *Amphiura* which is often equal in length to the entire oral plate ; a first oral tentacle scale usually present on the side of the oral plate, sometimes suppressed (in which case the oral papillae do not number less than four, unlike *Amphiodia*), or displaced so as to come more or less into series with the superficial oral papillae (which then often number only three) ; disc scaling usually complete but sometimes reduced on the lower side leaving more or less extensive areas of naked skin, the scales not armed with spinelets though some of the marginal scales may have inconspicuous prolongations ; the two radial shields of each pair variously related, most often contiguous only by their distal adradial corners but sometimes almost completely contiguous or conversely completely separate ; tentacle scales usually numbering one or two, sometimes suppressed beyond the basal segments which have a single scale.

AMPHIOPLUS subgenus ***AMPHIOPLUS*** Verrill

Type-species. *Amphiura tumida* Lyman, 1878.

Diagnosis. A subgenus of *Amphioplus* with the oral papillae numbering four and arranged in a concave, sometimes discontinuous, series not capable of closing the oral slit completely ; a first oral tentacle scale present, usually visible between and behind the first and second oral papillae so that the oral formula usually approximates to $\mathrm{m,m}\overset{\frown}{\mathrm{n,n}}\mathrm{m+t}$; the radial shields usually only contiguous distally, sometimes more fully contiguous or completely separate ; one or two tentacle scales.

The following nominal species are referable to the subgenus *Amphioplus* :

abditus (Verrill, 1871)
aciculatus Mortensen, 1936
acutus Mortensen, 1936
ancistrotus (H. L. Clark, 1911)
asterictus H. L. Clark, 1915
basilicus (Koehler, 1907)
conductus Koehler, 1922
coniortodes H. L. Clark, 1918
cuneatus (Lyman, 1878)
cyrtacanthus H. L. Clark, 1915
debilis (Koehler, 1904)
didymus H. L. Clark, 1938
echinulatus Mortensen, 1940
exsecratus (Koehler, 1905)
firmus (Koehler, 1904)
hexacanthus H. L. Clark, 1911
legatus Koehler, 1922
lobatus (Ljungman, 1867)
lucidus Koehler, 1922
macraspis (H. L. Clark, 1911)
magellanicus (Mortensen, 1936)
pectinatus Mortensen, 1933

personatus (Koehler, 1905)
platyacanthus Murakami, 1943
rhadinobrachius H. L. Clark, 1911
seminudus Mortensen, 1940
stenaspis H. L. Clark, 1938
stewartensis (Mortensen, 1924)
strongyloplax (H. L. Clark, 1911)
stratus Cherbonnier, 1963
tesselatus (Koehler, 1904)
thrombodes H. L. Clark, 1918
timsae Mortensen, 1926
tumidus (Lyman, 1878)—Type-species

In addition there are a number of species incertae sedis, either because of insufficiently precise description of their jaw armament, or else showing some characters more or less intermediate between the subgenera as defined above. These are as follows :

ailsaclarki Cherbonnier, 1957
archeri A. M. Clark, 1955
aurensis A. M. Clark, 1955
brachiostictus Tortonese, 1948
capax (Koehler, 1905)
causatus (Koehler, 1905)
cinctus (Koehler, 1914)
consors (Koehler, 1907)
difficilis (Duncan, 1887)
dispar (Koehler, 1897)
famula (Koehler, 1910)
glaucus (Lyman, 1879)
impressus (Ljungman, 1867)
intermedius (Koehler, 1905)
iuxtus Murakami, 1943
longirima Fell, 1952
magnificus (Koehler, 1907)
occidentalis Koehler, 1914
parviclypeus H. L. Clark, 1915
peregrinator (Koehler, 1912)
philohelminthius Ziesenhenne, 1940
psilochora (H. L. Clark, 1911)
refectus (Koehler, 1905)
signalis Koehler, 1930
textilis (Koehler, 1907)

Of these last nominal species, *A. archeri* at least may warrant distinction in a special taxon, either a subgenus, or possibly even a genus, since it diverges from *Amphioplus* sensu stricto in the direction of *Ophiophragmus*, having some development of marginal papillae, though the true extent of these remains to be seen from better samples with original as well as regenerating discs. Only the presence of the fourth oral papilla, which in this case arises from the side of the first ventral arm plate, distinguishes it from *Ophiophragmus*, of which the oral structure is of the *Amphiodia* (B)-type. Also in *A. archeri* the oral tentacle scale, or at least an additional papilla probably corresponding to this, is only rarely present (fig. 11), on one out of ten oral plates of the specimen figured.

Amphioplus psilochora is newly referred to the genus from *Amphiodia* and seems to occupy an isolated position. Its oral formula is m,mm,o +t, there being no fourth papilla at the distal end of the series, though the presence of the oral tentacle scale prevents its inclusion in *Amphiodia* ; in *Amphichilus* and *Unioplus*, also with only three papillae, it is the second one which is usually undeveloped. The affinities of *psilochora* may lie with *A. strongyloplax*, in which the fourth papilla can be reduced or lacking in some series or even entire specimens.

In addition to the species listed under the headings of the various subgenera of *Amphioplus* (pp. 48, 49, 52, 56–57) and those given as incertae sedis above, there are several other names which have been included in the genus which are now disposed of as follows :

agassizi Verrill, 1899b, referable to Ophiochitonidae (fig. 11b).
cythera A. H. Clark, 1949, referable to *Amphiactis* (fig. 11d,e, see p. 74).
diacritus Murakami, 1943, ? a synonym of *A. ancistrotus* (see A.M.C., 1965).
formatus (Koehler, 1905), not an amphiurid (fig. 11a, see pp. 61–62).
lorioli (Koehler, 1897), referable to *Amphiura*, with synonym *Amphiura ceramis* H. L. Clark, 1939 (see pp. 22–23).
luctator Koehler, 1922, ? a synonym of *Dougaloplus echinatus* (see p. 36).
modestus (Koehler, 1897), incomprehensibly referred from *Ophiochiton* (with which its affinities clearly lie) by H. L. Clark (1915).
nereis (Lyman, 1883), referable to Ophiochitonidae (fig. 11c).
papillatus (Lütken & Mortensen, 1899), referable to Ophiochitonidae.
trepidus (Koehler, 1904), referable to Ophiocomidae (see p. 37).

The presence of genital papillae in *A. agassizi*, *nereis* and *papillata* prohibits their inclusion in the Amphiuridae ; the narrow teeth with no infradental papillae exclude *A. cythera* and *formatus* ; the diminutive widely-separated radial shields distinguish *A. modestus* and *trepidus*, while the latter also has a group of apical tooth papillae rather than an infradental pair of oral papillae.

My studies to date lead me to the conclusion that *Amphioplus* occupies a central position among amphiurids, having affinities with other taxa as indicated in the diagram on p. 60.

Some notes on type-material in the Amsterdam Museum of some relevant " Siboga " species of Koehler follow, arranged in alphabetical order of species.

Amphioplus (Unioplus) conditus (Koehler)

Amphiura (*Amphioplus*) *condita* Koehler, 1905 : 46–47, pl. 5, figs. 9, 10.
Amphioplus conditus : H. L. Clark, 1915 : 257.

Locality. " Siboga " st. 89 ; Pulu Kaniungan, East Indies, 11 metres ; Amsterdam Museum, the holotype.

Descriptive notes. D.d. is 4 mm. The radial shields are c. $0{\cdot}9 \times 0{\cdot}3$ mm. = 3 : 1. The dorsal arm plates are more fan-shaped than shown in Koehler's figure and barely contiguous, if at all. There are only three oral papillae, the supposed second papilla being distinctly higher than the two distal papillae, the inner one of which is the largest ; the formula is m,om,m +t.

Amphioplus (Unioplus) confinis (Koehler)

Amphiura (*Amphioplus*) *confinis* Koehler, 1904 : 89, pl. 14, figs. 7, 8.
Amphioplus confinis : H. L. Clark, 1915 : 257.

Locality. " Siboga " st. 211, S of Celebes, 1158 metres ; Amsterdam Museum, four syntypes. St. 221, Flores Sea, 2798 metres ; two specimens. (The latter were not included in the " Siboga " report.)

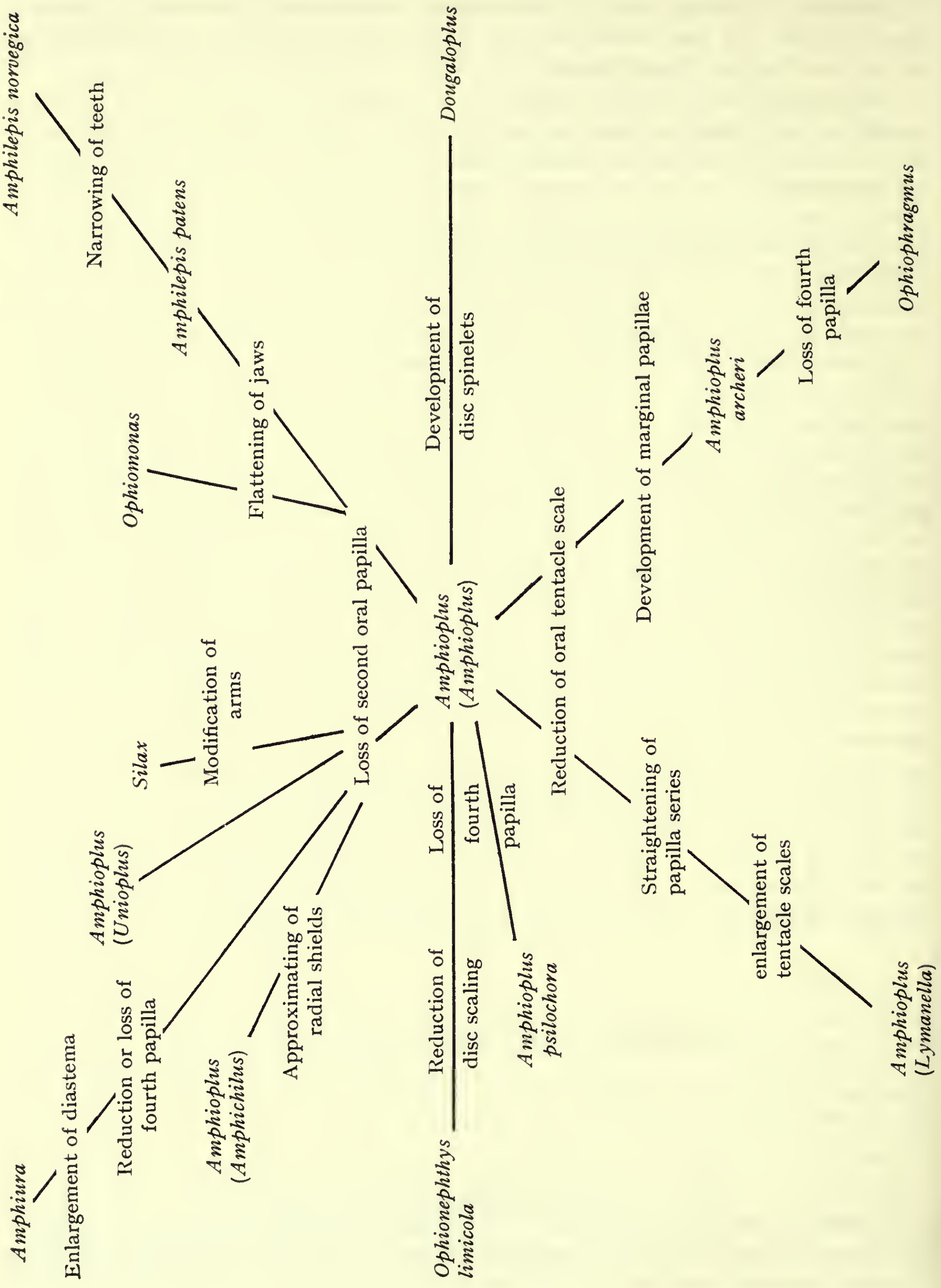
Descriptive notes. D.d. is 3·5–4·0 mm. The rosette is conspicuous ; the radial shields are long, divergent and completely separated, even distally. The disc scales are so thick as to produce an uneven profile. The dorsal arm plates are fan-shaped and not contiguous. The arm spines are conical and very acute, evenly tapering. The oral structure of the four syntypes shows some slight differences. One specimen has two jaws with the innermost oral papillae not infradental but offset to the sides of the lowest tooth, a third jaw has a close infradental pair, a fourth has three asymmetrical apical papillae and the fifth has three symmetrical papillae ; the first oral tentacle scale is superficial and in series with the oral papillae so that the formula is $m,(m = t)m\overset{\frown}{n,n}$; the adoral shields are widely contiguous and the oral shields are triangular with a slightly convex distal edge but the distal part distinctly hollowed. A second specimen has a close infradental pair of papillae on each jaw and the lowest tooth above may have a conical apex ; the oral tentacle scale is superficial for its whole length, even its base not being overlapped by the inner of the two distal papillae, while the outermost oral papilla barely makes contact with the adoral shield so that the formula is $m,(m = t)mm,$; the triangular oral shields have the distal side more convex but are less hollowed than in the first specimen. The third specimen has the infradental papillae more or less spaced on three jaws with a pointed tooth between, though the other teeth are broad as usual ; the oral tentacle scale is in continuous series with the oral papillae ; the inner of the two distal papillae is the largest one and the outer is small and seems to arise from the side of the first ventral arm plate rather than the edge of the adoral or the oral plate so that the formula is best expressed as $m,(m = t)m,,m$. The fourth syntype (in fact only three specimens were mentioned in the report but there is no way of telling whether one was added) is very like the second one with the infradental papillae regularly paired but the oral tentacle scale is less superficial and is overlapped distally by the middle oral papilla ; the oral shields are very wide and short and triangular in shape, as well as markedly hollowed. The smaller of the two specimens from station 221 has three infradental papillae on one jaw ; the larger specimen is poorly preserved ventrally.

Amphioplus (Amphioplus) exsecratus (Koehler)

Amphiura (*Amphioplus*) *exsecrata* Koehler, 1905 : 48–49, pl. 3, figs. 7, 8.
Amphioplus exsecratus : H. L. Clark, 1915 : 254.

Locality. " Siboga " ; Amboina reefs ; Amsterdam Museum, the holotype.

Descriptive notes. The oral structure is very like that of *Amphioplus* (*Lymanella*) *hastatus* with the four papillae in a straight series closing the oral slit and the third one the largest and blunt-conical in shape. However, the oral tentacle scale is present although concealed behind the papillae so that the formula is $m,m\overset{\frown}{n,n}m + t$.


Amphiura
Enlargement of diastema
Reduction or loss of fourth papilla
Amphilepis norvegica
Narrowing of teeth
Amphioplus (Unioplus)
Silax
Modification of arms
Ophiomonas
Amphilepis patens
Flattening of jaws
Amphioplus (Amphichilus)
Approximating of radial shields
Loss of second oral papilla
Ophionephthys limicola
Reduction of disc scaling
Loss of fourth papilla
Amphioplus (Amphioplus)
Development of disc spinelets
Dougaloplus
Amphioplus psilochora
Reduction of oral tentacle scale
Development of marginal papillae
Straightening of papilla series
enlargement of tentacle scales
Amphioplus archeri
Loss of fourth papilla
Ophiophragmus
Amphioplus (Lymanella)

The oral shields are shaped like the sole of a shoe, being elongated with a wide distal " heel " and a very short and obtuse proximal angle or " toe ". The two tentacle scales are very large, especially the ventral one. There are five arm spines proximally, the number falling to three. The upper surface is somewhat contorted ; the radial shields are probably narrow.

Amphioplus (Amphioplus) firmus (Koehler)

Amphiura (*Amphioplus*) *firma* Koehler, 1904 : 87–88, pl. 12, figs. 7, 8.
Amphioplus firmus : H. L. Clark, 1915 : 257.

Locality. " Siboga " st. 159, Molucca Is., 411 metres ; Amsterdam Museum, two syntypes.

Descriptive notes. D.d. is 4·5 mm. Both specimens have a very large central disc plate but no distinct primary radial scales though one appears to have distinctly enlarged primary interradials. In one the radial shields measure 1·2 : 0·4–0·5 mm. but in the other they are relatively a little broader ; the shields are completely separate, the scales between them not tapering outwardly ; interradially there are three to five scales between adjacent radial shields ; the dorsal arm plates are elliptical but slightly angled laterally ; two jaws have the pointed infradental papillae slightly separated and the tooth between them with a cusp ; the three distal oral papillae each side all arise from the side of the oral plate or else the narrow fourth one may abut on the first ventral arm plate so that the formula is m,(o)mmm(o),o +t or m,(o)mm,,m ; the first ventral arm plate is large and its proximal angle is quite superficial ; the tip of the first oral tentacle scale shows beyond the tip of the second oral papilla ; the third oral papilla is the largest. Both specimens have dark brown areas on the ventral side of the disc as if the scales are transparent.

" ***Amphioplus*** " ***formatus*** (Koehler)

fig. 11a

Amphiura (*Amphioplus*) *formata* Koehler, 1905 : 51–52, pl. 5, figs. 11–13, pl. 16, fig. 6.
Amphioplus formatus : H. L. Clark, 1915 : 257.

Locality. " Siboga " st. 310 or 312, N of Sumbawa, 73 or 274 metres ; Amsterdam Museum, the holotype.

Descriptive notes. D.d. is 12·5 mm. (Koehler estimated it as 12 mm.). The disc scaling is very fine, the rosette distinct but its plates very widely separated as in Koehler's figure ; there are some enlarged scales proximal to the radial shields, not shown by Koehler. The radial shields are contiguous for only about the distal fifth of their length ; their proportions are c. 2·2 : 0·8 mm. = 2·75 : 1 ; the proximal arm spines are 1·0–1·15 mm. long compared with an arm breadth of 1·07 mm. No oral tentacle scale could be found but behind the oral papillae there is a horizontal flange on the oral plate.

The relatively short arms with length only about three times the d.d., the large size, the narrow teeth with the two innermost oral papillae offset, the diminutive oral shields and the relatively long arm spines leave little doubt that this specimen is not an amphiurid at all ; however, at present I am not prepared to hazard a guess as to its true taxonomic position.

Amphioplus (Unioplus) gentilis (Koehler)

figs. 8r, 11g

Amphiura (*Amphioplus*) *gentilis* Koehler : 1904 : 86–87, pl. 16, figs. 8, 9.
Amphioplus gentilis : H. L. Clark, 1915 : 254.

Locality. "Siboga" st. 178, Molucca Is., 835 metres; Amsterdam Museum, several syntypes.

Descriptive notes. All the specimens are about the same size with d.d. 2–3 mm. The scales and plates are notably thickened and shiny, standing out in relief. In one specimen the radial shields are separated as shown in Koehler's figure but the six plates of the primary rosette may be closer than drawn, with only interstitial scales between their angles. The dorsal arm plates are all separate. The lowest tooth of this specimen has an abrupt median cusp on some jaws with the two innermost oral papillae offset rather than infradental ; their shape is conical. The two distal oral papillae each side are both partly or completely based on the edge of the adoral shield so that the formula is m,o,mm +t or $\mathrm{m,o\overset{\frown}{n,n}m}$ +t. The adoral shields are separated interradially in this specimen but in another they are broadly contiguous and the oral shields are much shorter. The latter also has the radial shields contiguous at their distal tips, the disc scales are flatter, also the outermost oral papilla is transparent or absent. Another has the oral shields intermediate between the two extremes. The infradental papillae may be almost contiguous and more rectangular in shape in some specimens, the first oral tentacle scale may be deeper in the oral slit and more rounded at the tip, the primary disc scales may be relatively larger and the radial shields contiguous distally for up to a quarter of their length. It is possible that not all these specimens are conspecific. Indeed a syntype in the collections of the Harvard Museum, no. M.C.Z. 3501 (fig. 11f) has been labelled (probably by H. L. Clark) "*Amphiactis* prob. *canescens*" and I agree that it is an *Amphiactis*, the teeth are acute.

Amphioplus (Unioplus) gratus (Koehler)

fig. 8k

Amphiura (*Amphiodia*) *grata* Koehler, 1904 : 85–86, pl. 18, fig. 6, pl. 19, fig. 7.
Amphiodia grata : H. L. Clark, 1915 : 249.

Locality. "Siboga" st. 211, S of Celebes, 1158 metres ; Amsterdam Museum, two syntypes.

Descriptive notes. The larger one has d.d. 10 mm. (Koehler gives 9 mm.).

The radial shields are 2·0 × 1·0 mm. and rather more angular than shown in Koehler's figure. There is a large central disc plate but the five widely spaced primary radials are barely larger than the other scales. The oral shields are rounded spearhead-shaped and hollowed in the middle ; the adorals are very convex. There are three oral papillae with which the oral tentacle scale is more or less in series, being superficial, so that the formula is m,(m = t)m,m. The outermost oral papilla is the widest and rectangular in shape. The dorsal arm plates have a slight median distal angle. The smaller syntype has d.d. 8 mm. It has the oral tentacle scale superficial on only three half-jaws so that the usual formula is m,om,m +t.

Amphioplus impressus (Ljungman)

fig. 9l, m

Amphipholis impressa Ljungman, 1867b : 314.
Amphiura (*Amphioplus*) *cesarea* Koehler, 1905 : 44–45, pl. 5, figs. 1, 2.
Amphioplus cesareus : H. L. Clark, 1915 : 257.
Amphioplus impressus : H. L. Clark, 1915 : 258 ; Koehler, 1922 : 174–176, pl. 64, figs. 3, 4 ; 1927a : 16–19, pl. 2, fig. 10, pl. 3, fig. 1.
Amphichilus cesareus : Koehler, 1930 : 119.

Localities. "Siboga" st. 294 ; off Timor, 73 metres ; Amsterdam Museum, two syntypes of *Amphiura cesarea*. Mortensen, 1922 ; Kei Is., 20 metres ; B.M. 1949.8.15.16, one specimen. "Albatross" st. 5371 ; Philippine Is., 152 metres ; U.S.N.M. 41171, one specimen.

Descriptive notes. The larger of the syntypes of *Amphiura cesarea* has d.d. 6·5–7·5 mm., the disc being distorted ; its radial shields are c. 1·15 × 0·5 mm. = 2·3 : 1 and contiguous for about three-quarters of their length. The smaller specimen has d.d. 5·5 mm. and its radial shields are also 1·15 mm. long but slightly narrower with the ratio 2·5 : 1. The rosette is distinct in both, with one row of scales between the primary plates. The disc scales are all thin and flat so that the disc appears fairly smooth ; there are six or seven scales between the radial shields across the interradii in the larger specimen but only three to five in the smaller. The dorsal arm plates of the smaller specimen particularly show the median distal angle which is rather exaggerated in Koehler's figure. In the larger one the oral slits are completely closed by the straight rows of four papillae but the second papilla is always small and conical and more often than not lies slightly above the level of the other papillae and clearly represents the oral tentacle scale ; the formula is therefore m,(m = t)m$\overset{\frown}{N,N}$, the distalmost papilla being very broad and almost opercular, with only its distal end contacting the adoral shield. Koehler's figure shows the oral shields as too pear-shaped ; they are relatively small and rhombic with the distal lobe only a little more blunt than the proximal. The arm spines are unusually diminutive on the first three segments. The tentacle scales are of moderate to small size. In the smaller specimen the second oral papilla is almost perfectly in series with the other three.

Remarks. The Kei Islands specimen was identified as *Amphichilus cesareus* by

Koehler (1930), whereas the "Albatross" specimens in the Smithsonian Institution he determined as *Amphioplus impressus* (1922); in the meantime (1927a) he redescribed and figured the two syntypes of *A. impressus.* Comparison of all these reveals no significant difference between the two nominal species, as far as I can see. The disc scaling appears to stand out a little more in relief in Ljungman's types than in those of *cesarea* but this could easily be due to the shading effect of angled lighting for the photographs. The border of narrow rectangular scales around the disc shown in Koehler's pl. 3, fig. 1 (1927a) of one syntype of *impressus* and in his drawing of one of *cesarea* (1905, pl. 5, fig. 1) is an unusual and distinctive feature. Another significant resemblance is the form of the first ventral arm plate; in nearly all amphiurids this inclines more or less gradually up into the oral slit, especially at its proximal end. In the types of both *impressus* and *cesareus* and the other specimens seen by me its superficial part is horizontal, ending proximally in an abrupt angle from which it passes vertically into the oral slit. I am convinced therefore that only a single species exists and that *Amphiura cesarea* is a synonym of *Amphioplus impressus.*

As for the precise position of the species within *Amphioplus,* without a larger sample I find this hard to determine. Apart from the one syntype of *A. cesarea* none of the specimens I have seen have the second oral papilla inset and it is difficult to ally them with *Amphichilus trichoides,* although the second papilla must represent the first oral tentacle scale. For the present at least I propose to leave the species in *Amphioplus* sensu stricto.

Amphioplus (?Amphioplus) intermedius (Koehler)

Amphiura (Amphioplus) intermedia Koehler, 1905 : 42, pl. 4, figs. 14, 15.
Amphioplus intermedius : H. L. Clark, 1915 : 258.

Locality. "Siboga" st. 77, Borneo Bank, 59 metres; Amsterdam Museum, the holotype.

Descriptive notes. D.d. is 4 mm. The radial shields are much more fully contiguous than is suggested by Koehler's figure, only the proximal tips being separated by a narrow V-shaped scale; their measurements are 1·0 × 0·25 mm. The fourth and outermost oral papilla is twice as wide as the third, while the second papilla is conical but perfectly in series with the other three. Together they form a straight series completely closing the oral slit so that it is impossible to see if there is an additional oral tentacle scale present above the series.

Amphioplus (Amphioplus) personatus (Koehler)

Amphiura (Amphioplus) personata Koehler, 1905 : 47–48, pl. 5, figs. 7, 8.
Amphioplus personatus : H. L. Clark, 1915 : 258.

Locality. "Siboga" st. 50, E of Flores, 40 metres; Amsterdam Museum, the holotype.

Descriptive notes. D.d. is 6 mm. The radial shields are 1·6 × 0·4 mm. The distal lobe of the oral shields is wider than is shown in Koehler's figure. The infradental papillae are huge, while the fourth and outermost papilla is very small and inconspicuous, apparently partly joined to the first ventral arm plate. The oral formula can be expressed as $\mathrm{M,om}\overset{\frown}{\mathrm{n,n}}\overset{\frown}{\mathrm{n,n}}$ +t, since the inconspicuous oral tentacle scale is placed well above the first and second papillae between which there is a space. The adoral shields almost meet radially as well as meeting interradially.

Amphioplus (?Amphioplus) refectus (Koehler)

Amphiura (*Amphioplus*) *refecta* Koehler, 1905 : 52–53, pl. 6, figs. 3, 4.
Amphioplus refectus : H. L. Clark, 1915 : 258.

Locality. "Siboga" st. 193, Molucca Is., 22 metres ; Amsterdam Museum, the holotype.

Descriptive notes. The holotype is somewhat decalcified. The edge of the disc is armed with a series of acute or slightly thorny spinelets. The radial shields are divergent for the proximal half to two-thirds of their length. The condition of the specimen makes it difficult to tell if the oral tentacle scale is present ; the oral formula is otherwise $\mathrm{m,m}\overset{\frown}{\mathrm{n,n}}\mathrm{m}$ (or m,mm,m). The tentacle scales are moderate in size.

Amphioplus (Unioplus) repositus (Koehler)

fig. 8m

Amphiura (*Amphiodia*) *reposita* Koehler, 1905 : 40–41, pl. 4, figs. 12, 13.
Amphiodia reposita : H. L. Clark, 1915 : 250.

Locality. "Siboga" st. 89, 11 metres ; Amsterdam Museum, three syntypes.

Descriptive notes. All three have d.d. c. 6·5 mm. In one specimen the second oral papilla is the largest and may have a double peak ; it arises mainly from the side of the oral plate so that the formula is $\mathrm{m,o}\overset{\frown}{\mathrm{n,n}}\mathrm{m}$ +t (fig. 8m). However, in another specimen the second papilla arises from the edge of the adoral shield so that the formula is m,o,mm +t, more like the condition shown in Koehler's figure. The radial shields are almost contiguous at their distal ends ; their adradial sides are straight and each measures c. 1·3 × 0·43 mm. The ventral disc scaling is very obscure.

Amphioplus (Unioplus) servatus (Koehler)

fig. 8p

Amphiura (*Amphiodia*) *servata* Koehler, 1904 : 84–85, pl. 15, figs. 6–8.
Amphiodia servata : H. L. Clark, 1915 : 250.

Locality. "Siboga" st. 262, W of Aru Is., 560 metres ; Amsterdam Museum, the holotype.

Descriptive notes. D.d. is 5 mm. The radial shields are c. 1·25 × 0·43 mm. and are neither so long nor so much separated as Koehler's figure shows. Nine of the series of oral papillae consist of three, with a formula of m,om,m +t but on the tenth there is an additional papilla in the space between the first two and the formula is m,mm,m +t. The first ventral arm plate has a markedly concave inner side.

Amphioplus (Lymanella) spinulosus (Koehler)

fig. 9v

Amphiura (*Amphioplus*) *spinulosus* Koehler, 1904 : 92–93, pl. 17, figs. 7, 8.
Amphioplus spinulosus : H. L. Clark, 1915 : 258.

Locality. " Siboga " st. 306, off Flores, 247 metres ; Amsterdam Museum, the holotype. St. 319 (omitted from report but added MS in Amsterdam Museum copy) ; Amsterdam Museum, one paratype.

Descriptive notes. The holotype has d.d. 5 mm. The primary rosette is distinct and there is a V-shaped scale between the proximal ends of each pair of radial shields. The scales of the uppermost ventral row, which lie around the dorsal disc margin as preserved, have their edges prolonged into usually single spine-like processes. The paratype has d.d. 4 mm. The radial shields are oval, 0·8 × 0·46 mm., and hardly separated even at their proximal ends. There are six or seven scales between the adjacent radial shields interradially. The primary rosette is not distinct. The series of marginal spinose processes (fig. 9v) is better preserved than in the holotype and is situated towards the ventral side of the margin. Some of the processes have a forked tip. The arms are distinctly rounded carinate above and the dorsal arm plates have the distal edge curved with a suggestion of a median angle. The arm spines are very acute. The tentacle scales are fairly large. The series of four oral papillae forms a straight row ; the third papilla is massive, truncated conical, while the others are rounded. They completely close the oral slits so that the occurrence of the oral tentacle scale cannot be ascertained. The oral shields are rather small and sunken in the middle, with a long distal lobe ; the adorals are very widely contiguous interradially.

Amphioplus capax (Koehler, 1905) and ***debilis*** (1904)

Unfortunately the type-material of both species is in poor condition orally, the holotype of *capax* being somewhat decalcified while the syntypes of *debilis* are either obscured with mud or else not conspecific with the specimen described and figured, having contiguous radial shields or only three oral papillae.

TRIODIA gen. nov.

Type-species. *Triodia abdita*[1] nov.

Diagnosis. A genus of Amphiuridae with three oral papillae, the second one running the length of the short oral plate and the third bordering the adoral shield ; with no oral tentacle scale developed, the oral formula is m,m,m —t ; a triangular supplementary adoral shield (possibly to be interpreted as one of a pair of supplementary oral shields) is present between each adoral and the genital slit ; the disc scales are unarmed ; the dorsal arm plates are not contiguous, even basally ; the ventral arm plates are somewhat swollen ; single crescentiform tentacle scales are present on a varying number of proximal arm segments, each scale bordering the lateral edge of the ventral arm plate and curving round on to the proximal part of the *following* lateral arm plate, the remaining tentacle pores lack scales.

Triodia abdita sp. nov.

fig. 10

Amphiura dalea (part) : Lütken & Mortensen, 1899 : 154–155, pl. 12, fig. 11 only. [Non *A. dalea* Lyman, 1879 : 27.]

Locality. " Albatross " st. 3361 ; 6°10'N : 83°6'W (Gulf of Panama), 2790 metres ; Museum of Comparative Zoology, Harvard, no. 1488, one specimen.

Description. D.d. is 14 mm. ; all the arms are broken within three joints of the base but there are some associated arm fragments, at least one of which belongs to this species.

The disc is covered with fine, well-defined scales, slightly larger and smoother around the radial shields and on the lower side towards the oral shields. The six plates of the primary rosette are enlarged but widely separated. In preservation the disc has tended to shrink into a crease in each interradius. In length the radial shields are just over a third of the disc radius, with length : breadth just under 3 : 1. The two shields of each pair are contiguous for about a quarter of their length distally, otherwise being separated by about four enlarged scales.

The oral papillae number three in each series. The infradental pairs of papillae are compact ; on one jaw three papillae take the place of two. The two other papillae each side also form contiguous series. The oral plates are unusually short and the second papilla is broad and occupies the whole length of the superficial edge of the oral plate. In shape it has some resemblance to an oral tentacle scale but it is completely superficial and perfectly in series with the two other papillae. The third and outermost papilla is equally broad but is based entirely on the edge of the adoral shield ; in one out of the ten series, this papilla is split into two. The second oral tentacle is visible behind the third papilla but there is no sign of a first oral tentacle scale on the vertical face of the oral plate. The oral formula can therefore be expressed as m,m,m —t. The oral shields are almost heptagonal, the distal part having three straight sides separated by distinct angles, while the four more proximal sides tend to merge into one another ; the length is greater than the breadth. The adoral shields just meet interradially ; distally they are very broad, separating the oral shield widely from the first lateral arm plate, also they are divided by an oblique suture forming a supplementary adoral shield adjacent to the genital slit.

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[1] The generic name is derived from the triangular tentacle scales, the series of three oral papillae and the triads of plates formed by the oral shields and adjoining supplementary adoral shields. The specific name signifies " hidden ", the holotype having for so long been submerged under another name in the collections of the Harvard museum. Gender: feminine.

The dorsal arm plates are very broad and short, the basal ones more than 2·5 times as broad as long and elliptical in shape; those on a detached arm fragment have become more pentagonal with the distal side flattened. All the plates are distinctly separated, the lateral arm plates meeting midradially for over a quarter of the segment length proximally. The ventral arm plates are relatively narrow, mostly slightly longer than broad. Their shape changes from rectangular on the first two segments to hexagonal by tapering of the proximal and distal ends. The large lateral arm plates bear eight or nine short tapering spines on the first free segments ; judging from the arm fragments the number rapidly falls to three. Even the longest spines are distinctly shorter than the segment. The middle spines are somewhat flattened.

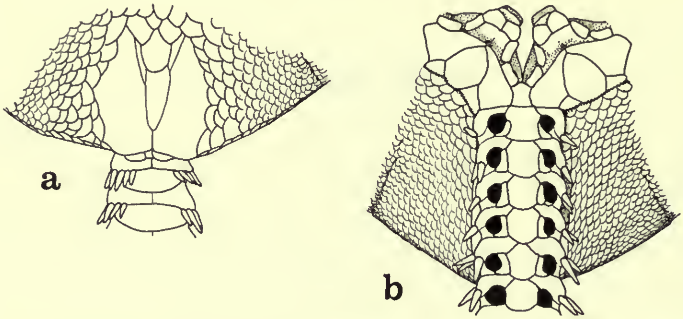

FIG. 10. *Triodia abdita* gen. & sp. nov., holotype, M.C.Z. 1488, " Albatross " st. 3361, Gulf of Panama, a. dorsal and b. ventral views of part of disc and an arm base.

On about the first five segments a crescent-shaped tentacle scale corresponds to each pore, running along the side edge of the ventral arm plate and curving around distally on the proximal side of the following lateral arm plate. The extent of the segments with scaled pores is clearly variable since one arm fragment has them at its proximal end although the number of arm spines has dropped to as little as four. On the other arm segments the large pores are naked.

REMARKS. This specimen was labelled *Amphioplus dalea* when I saw it in 1953, with a double query of the name added by H. L. Clark. Although in many ways it is similar to the other specimens which Lütken and Mortensen named *Amphiura dalea*, notably in the disc scaling, radial shields, the absence of tentacle scales from most arm pores (though this seems not unusual in deep-water amphiurids) and the non-contiguous dorsal arm plates (again a feature of many deep-water species), the coincidence of the modified oral structure, including the papillae and the adoral shields, and the unusual shape of the tentacle scales make it necessary to distinguish the specimen.

Of the other " Albatross " specimens, most have the oral formula approximating to m,(m = t)m,m. Three of the four from station 4670 have no tentacle scales at all and the fourth only has three or four proximal segments with single shorter scales restricted to the sides of the ventral arm plates. Those from station 4493 have more triangular oral shields, much wider distally ; also they have only three or four arm spines, even at d.d. c. 14 mm. Their identification is probably correct.

[AMPHILEPIDIDAE]

Amphilepididae Matsumoto, 1915 : 66 ; 1917 : 144–146 ; Fell, 1960 : 23 ; Spencer & Wright, 1966 : U100.
Amphilepididae : Koehler, 1922 : 202 ; Mortensen, 1927 : 222 ; 1933b : 372.
Amphilepidées : Koehler, 1930 : 132.

When established by Matsumoto this family included *Amphilepis* Ljungman, 1867b with the second oral tentacle pore opening outside the mouth, also *Amphiactis* Matsumoto, 1915 (non Verrill, 1867) and *Ophiochytra* Lyman, 1880 with this pore concealed inside the slit.[1] Most of Matsumoto's diagnosis appears to have been derived from *Amphiactis umbonata*, probably the only species personally studied by him. The main point of resemblance between *Amphilepis* and *Amphiactis* appears to be in the oral structure as seen in internal (dorsal) view, shown by a comparison of fig. 1c or Lyman's pl. XL, fig. 19[2] and Matsumoto's pl. III, fig. 7 ; these show that both have unusually reduced lateral wings to the oral frames. Regardless of this, H. L. Clark (1918), Mortensen (1927) and A. H. Clark, (1949) remove *Amphiactis* from the Amphilepididae and ally it with *Ophiactis*, while Fell (1960), followed by Spencer & Wright (1966), even adopt H. L. Clark's short-lived idea of *Amphiactis* as a synonym of *Ophiactis*, expressed in 1915 before due consideration. Only Koehler (1922 and 1930) seems to have retained the genus in the family Amphilepididae, mistakenly in my view since the arm structure particularly is very similar to that of *Ophiactis*, though I am sure the differing jaw structure warrants a generic distinction.

The removal of *Amphiactis* drastically undermines the validity of the Amphilepididae by implying that the reduction of the lateral wings of the oral frame is a character of lesser taxonomic weight, probably of generic value only, though Matsumoto's figures show marked variation from one species to another even within the same genus.

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[1] In fact Matsumoto was mistaken about this character as far as the type-species of **Ophiochytra,** *O. epigrus* Lyman, 1880, is concerned, the second oral pore being superficial in the holotype and only recorded specimen. *Ophiochytra* is not closely related to either *Amphilepis* or *Amphiactis* and I do not know why Lyman in his " Challenger " report placed it between *Ophiostigma* and *Ophiocentrus* (both Amphiurids according to Ljungman (1867b) and subsequent authors). With its short arms covered largely by the lateral arm plates, few peglike arm spines, very firm convex disc and strong oral skeleton and diminutive radial shields, I consider that it is a member of the Ophiurinae.

[2] It should be noted that Mortensen (1933b) has re-identified Lyman's " Challenger " specimens as *Amphilepis ingolfiana*, though this is very closely related to the type-species, *A. norvegica*.

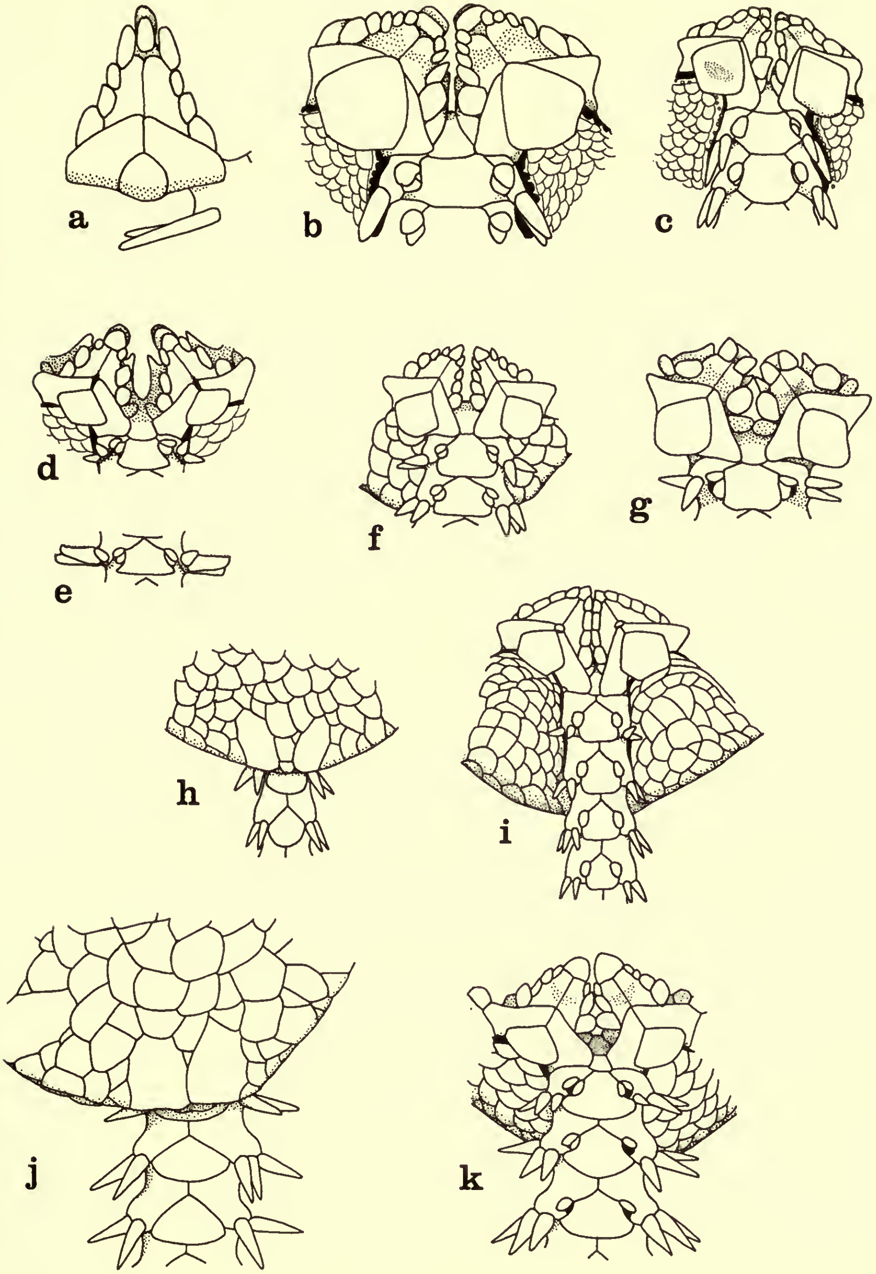
The affinities of *Amphilepis* are clearly with the Amphiuridae, as mentioned above (p. 37) under the heading of *Amphioplus*. It is quite easy to derive the jaw form of *Amphilepis norvegica* from that of *Amphioplus* via *Ophiomonas* (formerly *Amphilepis*) *protecta* and *Amphilepis patens* by progressive flattening of the jaws, bringing the second oral tentacle pore into a superficial position while the apex of the jaw and the teeth themselves become narrower, the two infradental papillae becoming slightly offset laterally with their bases inclined with respect to one another and at the same time come into series with the now superficial extended and subdivided first oral tentacle scales which have come to assume the function of the more or less reduced (ultimately absent) distal oral papillae (or second oral tentacle scales). I find Lyman's description of the oral structure of *Amphilepis* as stouter than that of most amphiurids very surprising. On the contrary it appears to me to be much more delicate, though this is especially noticeable in lateral view of the jaws (fig. 1a, d), which Lyman did not illustrate. [It should be noted that Murakami's remarks about the jaw structure of the Amphilepididae (1963), being based on *Amphilepis diastata*, are also misleading since the species is more closely related to *Amphiura diomediae* than to *Amphilepis norvegica* ; see p. 40.]

In view of the series of species bridging the gap between *Amphioplus* and *Amphilepis*, as far as jaw structure goes, I find it difficult to maintain the latter as representative of a distinct family. Accordingly I propose to reduce the rank of the Amphilepididae to that of a subfamily of the Amphiuridae.

AMPHILEPIS Ljungman

Amphilepis Ljungman, 1867b : 322 ; Lyman, 1882 : 149 ; H. L. Clark, 1915 : 244. Type-species : *Amphiura norvegica* Ljungman, 1864.

FIG. 11. a. " *Amphioplus* " *formatus* (Koehler), Amsterdam Museum, holotype, " Siboga " st. 310 or 312, off Sumbawa, E Indies, showing narrow teeth and very long arm spines ; b. " *Amphioplus* " *agassizii* Verrill, M.C.Z. 1261, holotype, off St. Lucia, W Indies ; c. " *Amphioplus* " *nereis* (Lyman), M.C.Z. 1260, holotype, off Montserrat, W Indies (b and c showing chilophiurid-type distal oral tentacle scale and genital papillae) ; d and e. *Amphiactis cythera* (A. H. Clark), U.S.N.M. E.6916, syntype, Hawaiian Is., e. the second free arm segment showing serrated arm spines ; f. *Amphiactis* sp. ?*canescens* (Lyman), M.C.Z. 3501, syntype of *Amphioplus gentilis* (Koehler) but not conspecific with most other types, " Siboga " st. 178, N. of Ceram, E Indies ; g. *Amphioplus* (*Unioplus*) *gentilis* (Koehler), Copenhagen Museum, Kei Is. Expedition st. 23 (see also fig. 8r) ; h and i. " *Amphiactis* " *astarte* A. H. Clark, U.S.N.M. E.7021, holotype, Hawaiian Is. ; showing chilophiurid-type distal oral tentacle scale ; the oval at the interradial apex of the adoral shields is an erect papilla, there is also a small nodule at the distal abradial corner of each shield not mentioned by A.H.C. ; j and k. *Amphiactis lycidas* A. H. Clark, U.S.N.M. E.7019, holotype, Hawaiian Is., the disc rather distorted.


a
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c
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k

Thirteen species have been referred to *Amphilepis*, namely :

antarctica Koehler, 1907
diastata Murakami, 1942
gymnopora Hertz, 1927
ingolfiana Mortensen, 1933b
mobilis Koehler, 1904
norvegica (Ljungman, 1864)
papyracea Lyman, 1879
patens Lyman, 1879
platytata H. L. Clark, 1911
protecta Koehler, 1904
remittens Koehler, 1922
scutata Mortensen, 1933a
tenuis Lyman, 1879

Of these, *A. protecta* has been referred to *Ophiomonas* by Djakonov (1952) and *diastata* to *Amphiura* by me (1965), while Madsen (1967) suspects that *gymnopora* will prove to be a synonym of *Amphiura belgicae.* Among the remainder, **Amphilepis infolfiana, mobilis, platytata** and **scutata** are closely related to the type-species, *A. norvegica*, having relatively narrow teeth, the more superficial ones at least pointed. The affinities of **Amphilepis antarctica** are uncertain, the holotype and only recorded specimen having d.d. only 2·5 mm. It is unusual in having the radial shields no bigger than the disc scales. Koehler's figures are so diagrammatic that it is impossible to determine its relationships. The holotype and only known specimen of **Amphilepis tenuis** is very badly decalcified and few of its characters are still distinguishable ; nor were Lyman's figures of it very good. However, it appears to have relatively broad squared-off teeth, in which it resembles **Amphilepis gymnopora,**[1] **papyracea, patens** and **remittens**, though in all these the ventralmost one may be more or less rounded or with a small median cusp and the apex of the jaw is also broad, the proportions and positions of the associated papillae and lowest tooth being somewhat variable. In some of these species there may be a superficial median apical papilla (e.g. in the two syntypes of *A. gymnopora* on some jaws) or the first oral papilla of each side may approximate to its partner and occupy an infradental position (e.g. in the left hand jaw shown of the holotype of *A. patens* in fig. 8c). In the case of *A. remittens* at least this blunting of the apex of the jaw is carried so far that the bases of the two innermost papillae, which are truly infradental, are tangential rather than oblique and I think it may be better referred to *Ophiomonas* like *A. protecta.* Unfortunately the holotype, which I have seen, is in poor condition and the details of the oral structure are difficult to make out. One other species, **Amphiura pycnostoma** H. L. Clark, 1911, should be added to this group of species of *Amphilepis.* The holotype in the Smithsonian Institution has the elongated oral tentacle scales superficial, as indeed H. L. Clark's figure suggests.

With only the holotypes of *Amphilepis patens* and *papyracea* to work on I am unable to compare the internal structure of any of these four species with that of *Amphilepis norvegica.* There is however, one obvious difference in *A. patens*, namely that it has long genital slits, though I do not think this is true of *papyracea.* A proper assessment of the relationships of these four species to those of *Amphilepis* sensu stricto (i.e. including *norvegica, infolfiana, mobilis, platytata* and *scutata*) must await further material.

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[1] Hertz describes the teeth of *A. gymnopora* as pointed but this is not supported by her photograph, which shows the apex of the jaw as relatively broad and blunt ; possibly the most superficial tooth is pointed.

Family **OPHIACTIDAE**

HISTAMPICA[1] nom. nov.

Amphiactis Matsumoto, 1915 : 66–67 ; 1917 : 146–147 ; H. L. Clark, 1918 : 294 (discussed under heading of *Ophiactis*) ; Koehler, 1922 : 204 ; A. H. Clark, 1949 : 29. Type-species : *Amphiactis umbonata* Matsumoto, 1915. Non *Amphiactis* Verrill, 1869, Coelenterata.

Unfortunately the generic name *Amphiactis* as used by Matsumoto is preoccupied and must be replaced.

As noted in the discussion above of Matsumoto's family Amphilepididae, Fell (1960) followed H. L. Clark's short-lived idea (1915, revoked in 1918) that *Amphiactis* is a synonym of *Ophiactis*. I consider that, on the contrary, it is more widely marked-off from *Ophiactis* than *Amphioplus* is from *Amphiura*, indeed almost as remote as *Amphilepis* is from *Amphiura* ; not only are there four or five oral papillae in each series rather than one or sometimes two, as found in *Ophiactis*, but also the teeth of *Amphiactis* are narrowed in a comparable fashion to those of *Amphilepis*, with which Matsumoto related it. I regard this as a convergent modification, not a sign of affinity. The internal structure of *Amphiactis* and *Ophiactis* is very different, judging from Matsumoto's studies.

The following nominal species have been referred to *Amphiactis* :

Amphiura canescens Lyman, 1879
Ophiactis dissidens Koehler, 1904
Amphiura duplicata Lyman, 1875
Ophiactis parata Koehler, 1904
Amphiura partita Koehler, 1897
Amphiura patula Lyman, 1879
Amphiactis umbonata Matsumoto, 1915 type-species
Ophiactis pectorale Lyman, 1880
Ophiocnida picteti de Loriol, 1893
Amphiactis astarte A. H. Clark, 1949
Amphiactis lycidas A. H. Clark, 1949.

The first seven were included by Matsumoto, followed by H. L. Clark who added *pectoralis* and *picteti* (the latter conditionally) and the last two by A. H. Clark.

As mentioned on p. 41 **Amphiura patula** Lyman is an *Amphioplus*, the apex of the jaw being broad, the additional median third infradental papilla being a peculiarity of the holotype and not shared by the paratype.

I have examined the holotype of **Ophiactis pectorale** and find that its jaw structure and interradially-folded disc accord not with the Ophiactidae but with certain members of the family Ophiacanthidae ; also it possesses the very distinctive diminutive hooks on the upper parts of the lateral arm plates characteristic of the ophiacanthid **Ophiodictys uncinatus** Koehler, 1922, though these were not noticed by Lyman. The two are certainly conspecific so *pectorale* is now referred to *Ophiodictys* with *uncinatus* becoming a synonym.

I think that H. L. Clark's misgivings about **Ophiocnida picteti** were justified ; since it has only two distal oral papillae each side, broad teeth with only a single infradental papilla and the disc with scattered spinelets, it is undoubtedly referable to *Ophiactis*.

Unfortunately I did not study the types of **Ophiactis parata** and **dissidens** when visiting Amsterdam. Koehler's figures are not sufficiently precise to fix the

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[1] *Histampica*, an anagram of *Amphiactis*. Gender: feminine.

relationships of the species with any certainty. The three tentacle scales on the proximal arm segments of *O. dissidens* and the rugose arm spines are features otherwise unknown in the Ophiactidae but which do occur in the Ophiacanthidae, to which the species must be referred ; it has some affinity with *Ophiophrura* H. L. Clark, 1911, except that the radial shields are distinct. *Ophiactis parata*, while not sharing these two characters, has an even closer resemblance to another ophiacanthid, namely **Ophiocopa singularis** Koehler, 1922, particularly the very short fully-contiguous radial shields with granular armament along their distal edges, unlike any ophiactid. I suspect that a comparison of specimens will prove the two to be conspecific, certainly they are congeneric.

Ophiactis partita, described earlier by Koehler, is evidently an *Amphiactis* in Matsumoto's sense, having been referred to the synonymy of *Amphiactis duplicata* by Koehler (1922).

I have seen the holotypes of both **Amphiactis lycidas** (fig. 11j, k) and *astarte* (fig. 11h, i) in the Smithsonian Institution. *A. lycidas* superficially recalls some ophiacanthids, especially in the proximal constriction of each arm segment, however, there seems no good reason for removing it from *Amphiactis*. **Amphiactis astarte** on the other hand resembles some of the Ophiolepidinae, notably *Ophiozonella*. Matsumoto has pointed out that *Amphiactis umbonata*, the type-species, has some resemblance in the disc scaling to *Ophiozona* (from which he split off *Ophiozonella*). However, in *A. astarte* an additional feature is that there is a fifth oral papilla at the distal end of the series (not mentioned by A. H. Clark) which is inclined up into the oral slit, a characteristic of the order Chilophiurida, which agrees with inclusion of the species in the Ophiolepidinae not the Ophiactidae, the latter being a family of the Gnathophiurida. I think that *astarte* should be referred to *Ophiozonella*.

Finally, the holotype of **Amphioplus cythera** A. H. Clark, 1949 (fig. 11d, e) is in my opinion congeneric with *Amphiactis umbonata*. It has rounded or tapering teeth, narrower than is usual in *Amphioplus* and there are no infradental papillae ; the structure of the arms is very like that of ophiactids.

The following species can therefore be included in *Histampica* : H. *canescens* (Lyman), *cythera* (A. H. Clark), *duplicata* (Lyman), *lycidas* (A. H. Clark) and *umbonata* (Matsumoto).

SUMMARIES OF PROPOSED TAXONOMIC CHANGES

I. Changes in Rank, New Taxa and Synonyms

A. GENUS-GROUP TAXA	*page*
Amphinephthys Fell a synonym of *Amphiura* Forbes	12
Icalia Fell a synonym of *Amphiura* Forbes	12
Pandelia Fell a synonym of *Amphiura* Forbes	12
Hemilepis Ljungman a synonym of *Amphiura* Forbes	12
Nullamphiura Fell a synonym of *Amphiura* Forbes	12
Monamphiura Fell a synonym of *Amphiura* Forbes	12
Ophiopeltis Düben & Koren reduced to a subgenus of *Amphiura* Forbes	12

Fellaria subgen. nov. of *Amphiura* for type *Ophionephthys octacantha* H. L. Clark	18
Ophionema Lütken reduced to a subgenus of *Amphiura* Forbes	19
Ophionephthys Lütken restricted to the type-species	20
Gymnodia Fell a synonym of *Amphiodia* Verrill	25
Diamphiodia Fell a synonym of *Amphiodia* Verrill	25
Amphiodia (*Amphispina*) validated by type-designation	25
Nullopholis Fell a synonym of *Amphipholis* Ljungman	31
Monopholis Fell a synonym of *Amphipholis* Ljungman	31
Amphistigma H. L. Clark a valid genus distinct from *Ophiostigma*	33
Amphiacantha Matsumoto pre-occupied, replaced by *Dougaloplus* nom. nov.	33
Amphichilus Matsumoto reduced to subgenus of *Amphioplus* Verrill	48
Unioplus Fell reduced to a subgenus of *Amphioplus* Verrill	48
Ailsaria Fell a synonym of *Amphioplus* Verrill	50
Lymanella subgen. nov. of *Amphioplus* for type *A. hastatus* Ljungman	51
Triodia gen. nov. for type *T. abdita* sp. nov.	67
Amphiactis Matsumoto preoccupied, replaced by *Histampica* nom. nov.	73

B. SPECIES-GROUP TAXA	*page*
Ophionephthys octacantha H. L. Clark designated type-species of *Amphiura* subgen. *Fellaria* nov.	18
Ophionephthys decacantha H. L. Clark a synonym of *A.* (*Fellaria*) *octacantha* (H. L. Clark)	18
Amphiura norae Benham and *abernethyi* Fell both synonyms of *A. correcta* Koehler	22
Amphiura ceramis H. L. Clark a synonym of *A. lorioli* (Koehler)	23
Amphiodia cyclaspis Djakonov a synonym of *A. craterodmeta* H. L. Clark	28
Amphipholis murex (Koehler) a synonym of *Ophiocnida loveni* (Ljungman)	31
Amphiacantha dividua Matsumoto a synonym of *Ophiocomella sexradia* (Duncan)	33
Amphioplus luctator Koehler ?a synonym of *Dougaloplus echinatus* (Ljungman)	36
Amphichilus cesareus (Koehler) a synonym of *Amphioplus impressus* (Ljungman)	45
Amphioplus praestans (Koehler) a synonym of *A.* (*Lymanella*) *laevis* (Lyman)	53
Amphioplus bocki Koehler ? a synonym of *A.* (*Lymanella*) *laevis* (Lyman)	53
Amphioplus megapomus H. L. Clark a synonym of either *A.* (*Lymanella*) *laevis* (Lyman) or of *A.* (*L.*) *andreae* (Lütken)	53
Amphioplus miyadii Murakami ? a synonym of *A.* (*Lymanella*) *laevis* (Lyman)	53
Amphioplus potens Koehler a synonym of either *A.* (*Lymanella*) *laevis* (Lyman) or of *A.* (*L.*) *andreae* (Lütken)	55
Ophiodictys uncinatus Koehler (Ophiacanthidae) a synonym of *O. pectoralis* (Lyman), referred from *Ophiactis*	73
Ophiactis parata Koehler ? a synonym of *Ophiocopa singularis* Koehler (Ophiacanthidae)	74

TRANSFERS OF SPECIES TO DIFFERENT GENERA (OR FAMILIES)[1]

Pre-1962 combination	Genus according to Fell	Genus according to A.M.C.
Ophionephthys africana Balinsky	*Ophiopeltis*	*Amphiura* (*Fellaria*)
Ophionephthys heptacantha Mtsn.	*Ophiopeltis*	*Amphiura* (*Fellaria*)
Ophionephthys iranica Mtsn.	*Ophiopeltis*	*Amphiura* (*Ophiopeltis*)

[1] Not exhaustive for Fell's larger subdivisions.

TRANSFERS OF SPECIES (*cont.*)

Pre-1962 combination	Genus according to Fell	Genus according to A.M.C.
Ophionephthys magellanica Mtsn.	*Ophionephthys*	*Amphioplus* (*Amphioplus*)[1]
Ophionephthys octacantha H.L.C.	*Ophiopeltis*	*Amphiura* (*Fellaria*)
Ophionephthys phalerata Lyman	*Ophionema*	*Amphiura* (*Ophiopeltis*)
Ophionephthys stewartensis Mtsn.	*Ophionephthys*	*Amphioplus* (*Amphioplus*)
Ophionephthys tenuis H.L.C.	*Ophionema*	*Amphiura* (*Ophiopeltis*)
Ophionema hexactis Mtsn.	—	*Amphiura* (*Ophiopeltis*)
Amphiura aestuarii Matsumoto	*Ophiopeltis*	*Amphiura* (*Ophiopeltis*)
Amphiura alba Mtsn. & other spp. ref. to	*Monamphiura*	*Amphiura* (*Amphiura*)
Amphiura crossota Murakami & other spp. ref. to	*Amphinephthys*	*Amphiura* (*Amphiura*)
Amphiura ecnomiotata H.L.C.	*Ophiopeltis*	*Amphiura* (*Fellaria*)
Amphiura fragilis Verrill & other spp. ref. to	*Icalia*	*Amphiura* (*Amphiura*)
Amphiura hinemoae Mtsn. & other spp. ref. to	*Pandelia*	*Amphiura* (*Amphiura*)
Amphiura psilopora H.L.C. & other spp. ref. to	*Nullamphiura*	*Amphiura* (*Amphiura*)
Amphiura pycnostoma H.L.C.	*Monamphiura*	*Amphilepis*
Amphiura semiermis Lyman & other spp. ref. to	*Hemilepis*	*Amphiura* (*Amphiura*)
Amphiura sinicola Matsumoto	—	*Amphiura* (*Fellaria*)
Amphiura vadicola Matsumoto	*Ophiopeltis*	*Amphiura* (*Fellaria*)
Amphipholis loripes Koehler	*Monopholis*	*Amphipholis* or *Amphiodia*
Amphipholis murmanica Djakonov	*Monopholis*	*Amphipholis*
Amphipholis nudipora A.M.C.	*Nullopholis*	*Amphipholis*
Amphipholis pentacantha H.L.C.	*Nullopholis*	*Amphipholis*
Amphipholis vitax Koehler	*Monopholis*	*Amphipholis*
Amphistigma minuta H.L.C.	*Ophiostigma*	*Amphistigma*
Amphiodia affinis (Studer)	*Amphiodia*	*Amphioplus*
Amphiodia assimilis (Ltk. & Mtsn.)	*Diamphiodia*	*Amphiura* (*Amphiura*)
Amphiodia caulleryi (Koehler)	*Diamphiodia*	? *Amphiura* or *Amphioplus* (*Amphichilus*)
Amphiodia fuscoalba (Brock)	—	*Acrocnida*
Amphiodia grata (Koehler)	*Diamphiodia*	*Amphioplus* (*Unioplus*)
Amphiodia ochroleuca (Brock)	*Diamphiodia*	*Amphioplus* (*Amphichilus*)
Amphiodia olivacea (Brock)	*Amphiodia*	*Ophiophragmus*
Amphiodia platyspina Nielsen	*Gymnodia*	*Amphiodia*
Amphiodia psilochora H.L.C.	*Gymnodia*	*Amphioplus*
Amphiodia reposita (Koehler)	*Diamphiodia*	*Amphioplus* (*Unioplus*)
Amphiodia servata (Koehler)	*Diamphiodia*	*Amphioplus* (*Unioplus*)
Amphiodia tabogae Nielsen	*Gymnodia*	*Amphiodia*
Amphiodia urtica (Lyman)	*Ophiophragmus*	*Amphiodia*
Amphiodia violacea (Lütken) & other spp. ref. to	*Diamphiodia*	*Amphiodia*
Ophiocnida echinata (Ljungman)	—	*Dougaloplus*
Ophiocnida picteti de Loriol	—	*Ophiactis*
Ctenamphiura sinensis A.H.C.	*Diamphiodia*	*Paracrocnida*
Amphiacantha acanthina (H.L.C.)	—	*Dougaloplus*
Amphiacantha amphacantha (McCl.)	—	*Dougaloplus*

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[1] Referred to *Amphioplus* by Castillo (1968).

TRANSFERS OF SPECIES (*cont.*)

Pre-1962 combination	Genus according to Fell	Genus according to A.M.C.
Amphiacantha formosa (Ltk.)	—	*Dougaloplus*
Amphiacantha gastracantha (Ltk. & Mtsn.)	—	*Dougaloplus*
Amphiacantha libera (Koehler)	—	*Dougaloplus*
Amphiacantha notacantha (Ltk. & Mtsn.)	—	*Dougaloplus*
Amphiacantha transacta Koehler	—	order Chilophiurida
Amphichilus daleus (Lyman)	—	*Amphioplus* (*Unioplus*)
Amphichilus intermedius (Koehler)	—	*Amphioplus*
Amphichilus trichoides Matsumoto	—	*Amphioplus* (*Amphichilus*)
Amphioplus aciculatus Mtsn.	*Unioplus*	*Amphioplus* (*Amphioplus*)
Amphioplus agassizi Verrill	*Amphioplus*	family Ophiochitonidae
Amphioplus andreae (Lütken)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus brachiostictus Tort.	*Amphiodia*	*Amphioplus*
Amphioplus caelatus Ely	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus capax Koehler	*Unioplus*	*Amphioplus*
Amphioplus cernuus (Lyman)	*Unioplus*	*Amphioplus* (*Unioplus*)
Amphioplus conditus (Koehler)	*Amphioplus*	*Amphioplus* (*Unioplus*)
Amphioplus confinis (Koehler)	*Amphioplus*	*Amphioplus* (*Unioplus*)
Amphioplus congensis (Studer)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus coniortodes H.L.C.	*Ailsaria*	*Amphioplus* (*Amphioplus*)
Amphioplus cyrtacanthus H.L.C.	*Ophionephthys*	*Amphioplus* (*Amphioplus*)
Amphioplus cythera A.H.C.	*Amphioplus*	*Histampica*
Amphioplus depressus (Ljungman)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus dispar (Koehler)	*Unioplus*	*Amphioplus*
Amphioplus echinulatus Mtsn.	*Ailsaria*	*Amphioplus* (*Amphioplus*)
Amphioplus falcatus Mtsn.	*Unioplus*	*Amphioplus* (*Unioplus*)
Amphioplus formatus (Koehler)	*Unioplus*	? not amphiurid
Amphioplus gentilis (Koehler)	*Amphioplus*	*Amphioplus* (*Unioplus*)
Amphioplus gibbosus (Ljungman)	—	*Amphioplus* (*Lymanella*)
Amphioplus glaucus (Lyman)	*Unioplus*	*Amphioplus*
Amphioplus hastatus (Ljungman)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus incisus (Lyman)	*Amphioplus*	*Amphioplus* (*Unioplus*)
Amphioplus integer (Ljungman)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus japonicus (Mats.)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus laevis (Lyman)	*Amphioplus*	*Amphioplus* (*Lymanella*)
Amphioplus lorioli(Koehler)	*Amphioplus*	*Amphiura*
Amphioplus lucidus Koehler	*Ophionephthys*	*Amphioplus*
Amphioplus macraspis H.L.C.	*Unioplus*	*Amphioplus* (*Amphioplus*)
Amphioplus modestus (Koehler)	—	*Ophiochiton*
Amphioplus nereis (Lyman)	*Amphioplus*	Ophiochitonidae
Amphioplus patulus (Lyman)	*Unioplus*	*Amphioplus* (*Unioplus*)
Amphioplus personatus (Koehler)	*Ailsaria*	*Amphioplus* (*Amphioplus*)
Amphioplus philohelminthius Zies.	*Unioplus*	*Amphioplus*
Amphioplus seminudus Mtsn.	*Ophionephthys*	*Amphioplus* (*Amphioplus*)
Amphioplus spinulosus (Koehler)	—	*Amphioplus* (*Lymanella*)
Amphioplus strongyloplax (H.L.C.)	*Unioplus*	*Amphioplus* (*Amphioplus*)
Amphioplus thrombodes (H.L.C.)	*Unioplus*	*Amphioplus* (*Amphioplus*)
Amphioplus trepidus (Koehler)	*? Silax*	Ophiocomidae
Amphilepis diastata Murakami	—	*Amphiura*
Amphilepis remittens Koehler	—	*? Ophiomonas*

TRANSFERS OF SPECIES (*cont.*)

Pre-1962 combination	Genus according to Fell	Genus according to A.M.C.
Amphiactis astarte A.H.C.	—	*Ophiozonella* (Ophiuridae)
Amphiactis canescens (Lyman)	—	*Histampica*
Amphiactis dissidens (Koehler)	—	*Ophiacanthidae*
Amphiactis duplicata (Lyman)	—	*Histampica*
Amphiactis lycidas A.H.C.	—	*Histampica*
Amphiactis pectorale (Lyman)	—	*Ophiodictys* (Ophiacanthidae)
Amphiactis umbonata Matsumoto	—	*Histampica*
Ophiochytra epigrus Lyman	—	*Ophiuridae*

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D. A. GRIFFITHS

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BY

DONALD ALISTER GRIFFITHS

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A FURTHER SYSTEMATIC STUDY OF THE GENUS *ACARUS* L., 1758 (ACARINA)

By D. A. GRIFFITHS

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1. INTRODUCTION

Virtually on the eve of the publication of my revision of the genus *Acarus* L., 1758 (Griffiths, 1964) I found a thriving population of the species here described as *Acarus nidicolous sp.n.* in the grounds of the Pest Infestation Laboratory. The chaetotaxy of the dorsum, in particular the length of setae *la* and d_1 to d_4, and the results of crossing it with the species of the *Acarus siro* complex was such that had this taxon been discovered earlier, some of the taxa which in the revision were placed as specimens *incertae sedis* would have been given specific status. More recently, Dr. van Eyndhoven, Dr. D. Furman and Dr. D. J. Johnston kindly presented me with *Acarus* material which they considered did not correspond to any of the forms included in the revision.

Thus, within a few months of completing a long study, it became necessary to prepare a second paper, as a consequence of which the number of species in the genus is almost doubled, an accurate reflection of the ever-changing situation in acarine taxonomy at this present time.

The descriptions which appear within follow the pattern used to re-describe *Acarus farris* Oudemans, 1905 in Griffiths, 1964. They were made with a new microscope and, as a result, I have discovered some omissions and some mistakes in my previous descriptions of the *Acarus* hypopi which I will amend here.

Firstly, a pair of supra-coxal setae are present in the motile and inert hypopal forms. They are situated above coxae I, respectively. In the motile hypopi they are similar in size and shape to the supra-coxal setae of *Acarus nidicolous* (Text-fig. 16). Those of *Acarus immobilis* Griffiths, 1964 are much shorter.

Secondly, in the motile *Acarus* hypopi and, so far this appears to be true for motile hypopi of many other genera within the family, the structure which I termed seta *ba* on tarsus I (see Text-figs. 10 and 21 of Griffiths 1964) is actually solenidion ω_3, seta *ba* is absent. This rule also applies to the inert hypopus of *A. immobilis*, the seta labelled *ba* in Text-fig. 28 of Griffiths 1964 is a minute solenidion ω_3

2. GENERIC CHARACTERS

The generic characters of the adult stage as given in Griffiths 1964 still stand. In addition, I am now satisfied that the morphology of the female reproductive system is sufficiently different from that of closely related genera for it to be used as a diagnostic character. It is described in Text-fig. 1.

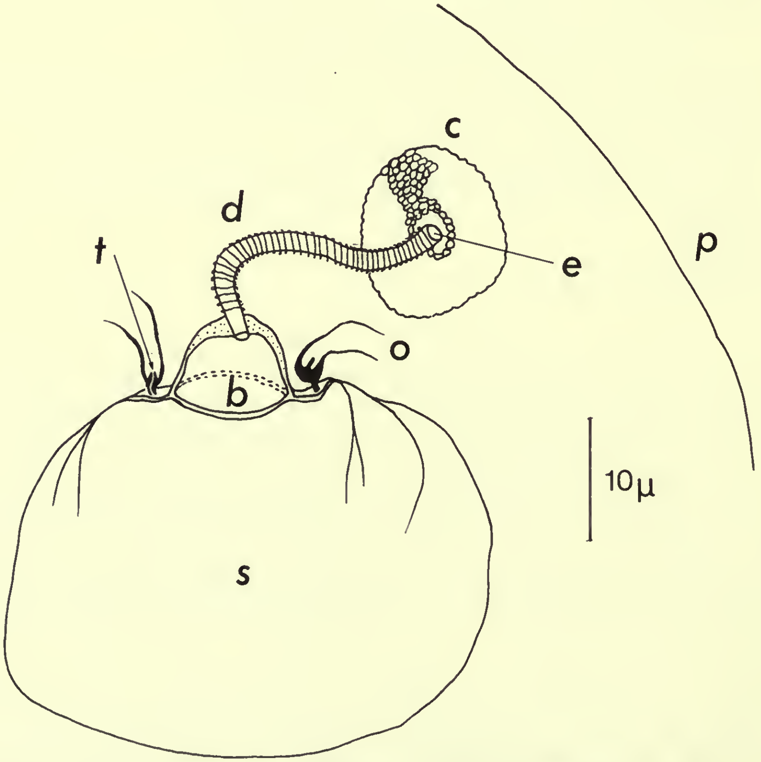


FIG. 1. *Acarus siro* L., ♀ reproductive system; p. posterior margin of body; c. chitinised, saucer-like depression in body wall; e. opening of expansible tube (d); b. chitinised, bell-shaped structure attached to which is a thin walled, dilatable sac (s) t. chitinised opening to thin walled oviduct (o).

Zatchvatkin 1941 (see p. 115 in the English Translation by Ratcliffe & Hughes 1959) stated that " the setae of the dorsal surface [in *Acarus* hypopi] are longer than in the hypopi of all other representatives of the family—*sc* [scapular setae] being particularly long. The fact that the hypopus of *A. nidicolous* sp.n., described herein, has short scapulars which barely reach the posterior margin of the propodosomal shield (Text-fig. 16) means that the relative length of the scapular setae can no longer be used as a diagnostic character at generic level. As more species are described, it is becoming increasingly difficult to find characters which can serve to separate motile hypopi of the family Acaridae into their respective genera. The practice of describing new species and especially new genera based solely on the hypopal form must be considered of doubtful benefit to acarine taxonomy.

3. MORPHOLOGICAL VARIATION

In my revision of the genus *Acarus* (Griffiths, 1964) material representing eight taxa was designated as specimens *incertae sedis* because, at the time, there was no way of determining whether the morphological differences exhibited by these taxa represented intra-specific or inter-specific variation. Material collected since 1964 and the results of nutritional experiments performed on sibling females of *A. siro* has now helped to clarify the position.

In Griffiths 1966 I showed that the tarsal length of adults varied according to the nutritional quality of the food they received during the pre-adult period. An example of this type of variation in a wild population is represented by Text-figures 23 and 24. Recently, I have examined the effect which high and low nutrient diets have upon the growth of the dorsal hysterosomal setae. Examples of the results obtained for groups of sibling females are illustrated in Text-figs. 2a and b. A poor diet (Fig. 2b) produces short, thin setae whereas a rich diet favours longer, thicker ones (Fig. 2a). Their length expressed as a percentage of the respective idiosomal length is given below.

Setal length as percentage of idiosomal length

Setae	♀ reared on poor food (Text-fig. 2b)	♀ reared on rich food (Text-fig. 2a)
d_1	4·6	8·6
d_2	7·7	15·6
d_3	9·4	14·4
d_4	9·2	15·9
la	6·2	10·8
lp	8·3	13·3
sa e	7·8	11·4

Seta d_2 shows the greatest variation. It is an interesting point that in the ecologically isolated species *Acarus gracilis* seta d_2 is much longer than d_1 or d_3 (Text-fig. 8) and serves to distinguish this species from all *Acarus* species.

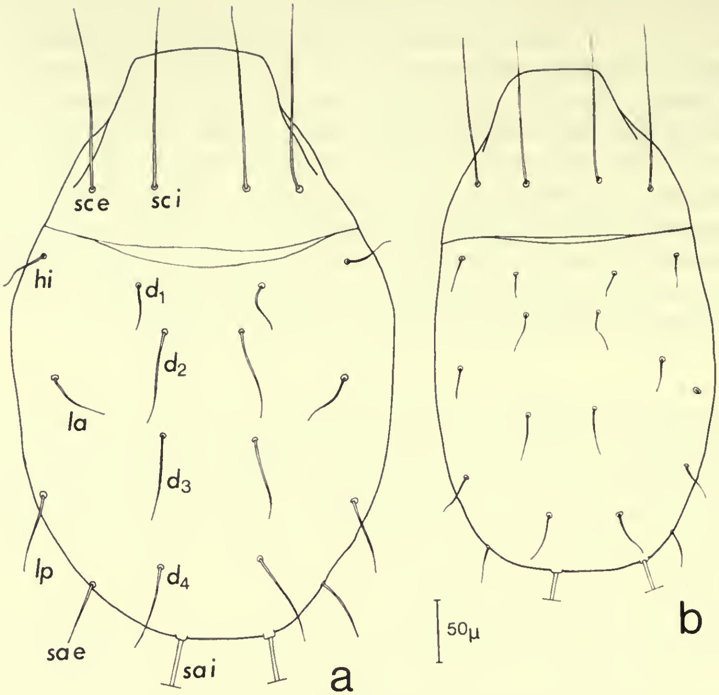

sce
sci
hi
d_1
d_2
la
d_3
lp
d_4
sae
sai
a
50μ
b

FIG. 2. *Acarus siro* L., idiosoma of sibling ♀♀'s illustrating variation in length of dorsal setae (d_1 to d_4), brought about by exposing pre-adult stages to (a) a rich diet and (b) a poor one.

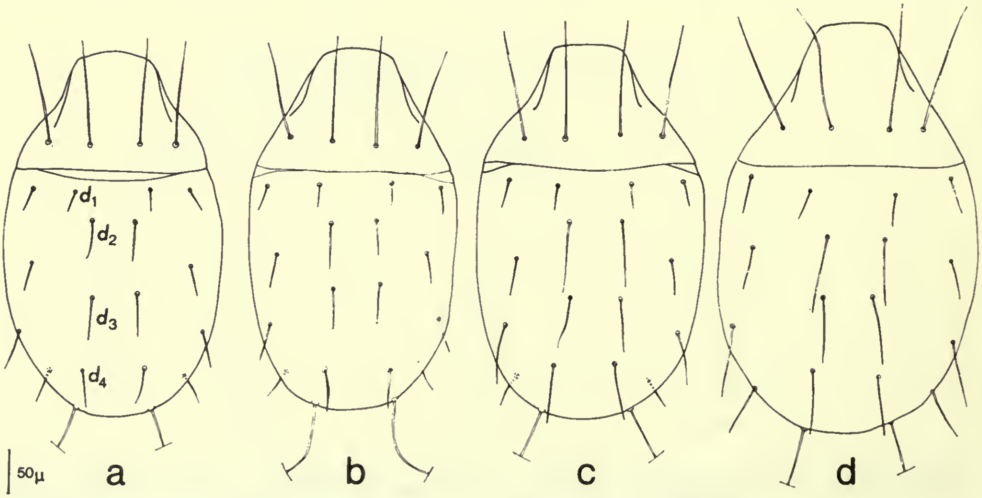

d_1
d_2
d_3
d_4
50μ
a
b
c
d

FIG. 3. *Acarus siro* L., idiosoma of ♀♀'s taken from a natural population, showing extreme range of variation in length of dorsal setae.

I have found one population of *A. siro* in which the length of the hysterosomal setae is extremely variable. This was taken from a bag of oatmeal which had been left in a garden shed for more than five years. The range of variation in setal length exhibited by the females of this population is illustrated in Text-fig. 3. It should be noted that in individuals with the longest setae, the tips of the d_3 dorsals overlap the bases of the d_4 pair. However, in the vast majority of the many populations of *A. siro* which I have examined, the length of the dorsal setae d_1 to d_4 is never as great as the distance between its base and the base of the dorsal seta immediately posterior to it.

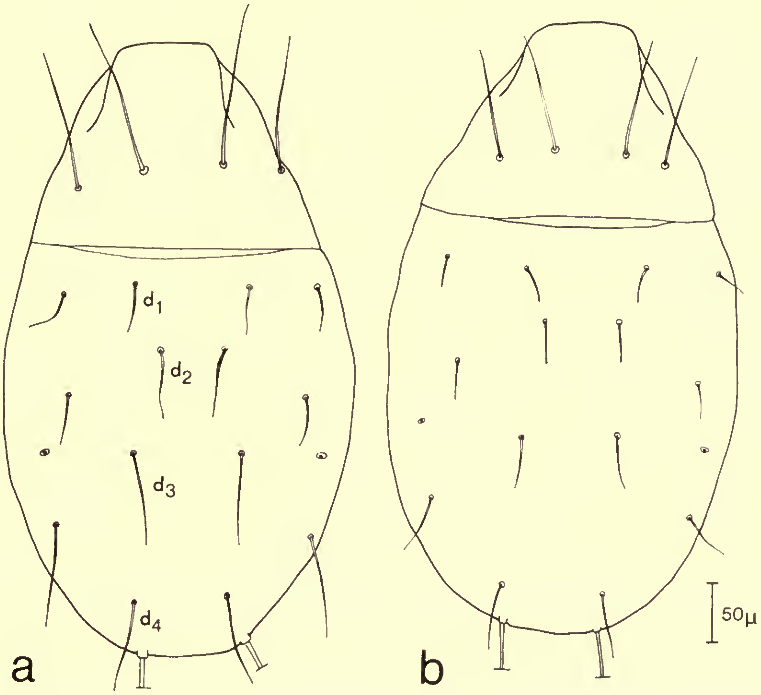


FIG. 4. *Acarus immobilis* Griffiths. Idiosoma of ♀♀'s taken from a seven year old stock laboratory culture, illustrating extremes of variation in length of dorsal setae (d_1 to d_4).

Some populations of *A. immobilis* and *A. farris* which I have obtained since 1964 also exhibit variation in dorsal setal length. But, so far, I have not found an individual of either species in which the length of seta d_2 or d_3 exceeds the distance between the base of d_2 and d_3 or d_3 and d_4. Text-figure 4 gives examples of the extremities of the range of variation found in a population of *A. immobilis*, cultured in the laboratory for seven years.

After studying many populations representing the *A. siro* species complex, I believe the tendency in most populations is towards short dorsal setae. But, at the extreme range of variation so far observed (i.e. in *A. siro*), the tips of the d_2 setae, when projected backwards in a straight line, often overlap the bases of pair d_3.

There is another group of species, described herein for the first time, in which the dorsal setae are usually long so that the tips of d_1, d_2 and d_3 distinctly overlap the base of the seta next in line (e.g. Text-fig. 9). But, in two species (*A. nidicolous*, which I have in culture and *A. macrocoryne*, known from two preserved populations) individuals can be found in which some dorsal seta are shorter than the distance separating the relevant bases (Text-fig. 5).

Previously, the shape of solenidion ω_1 on tarsus II was the only diagnostic character which, by itself, could be used to distinguish all the species in the genus. Plates I, II and III illustrate that this is now no longer possible.

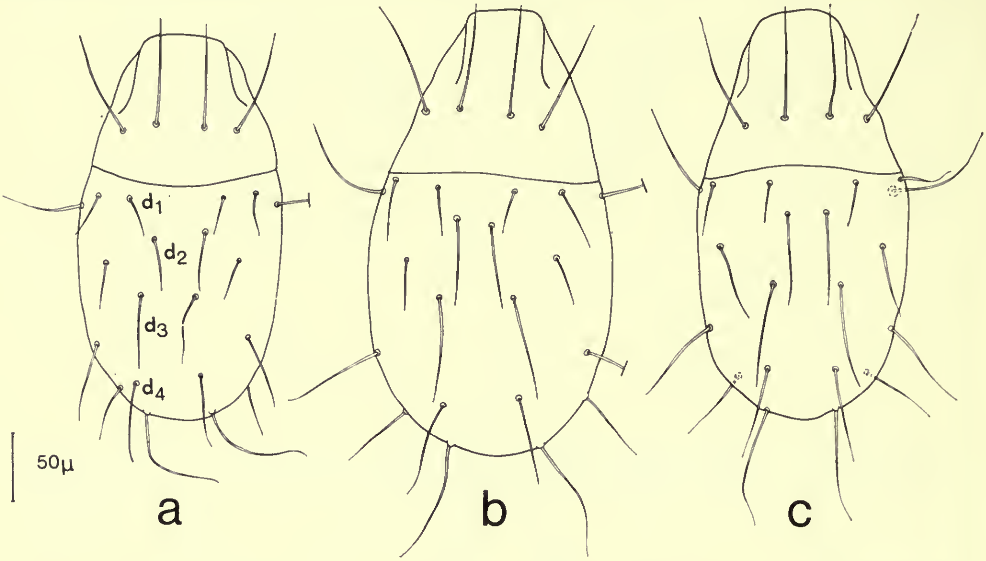
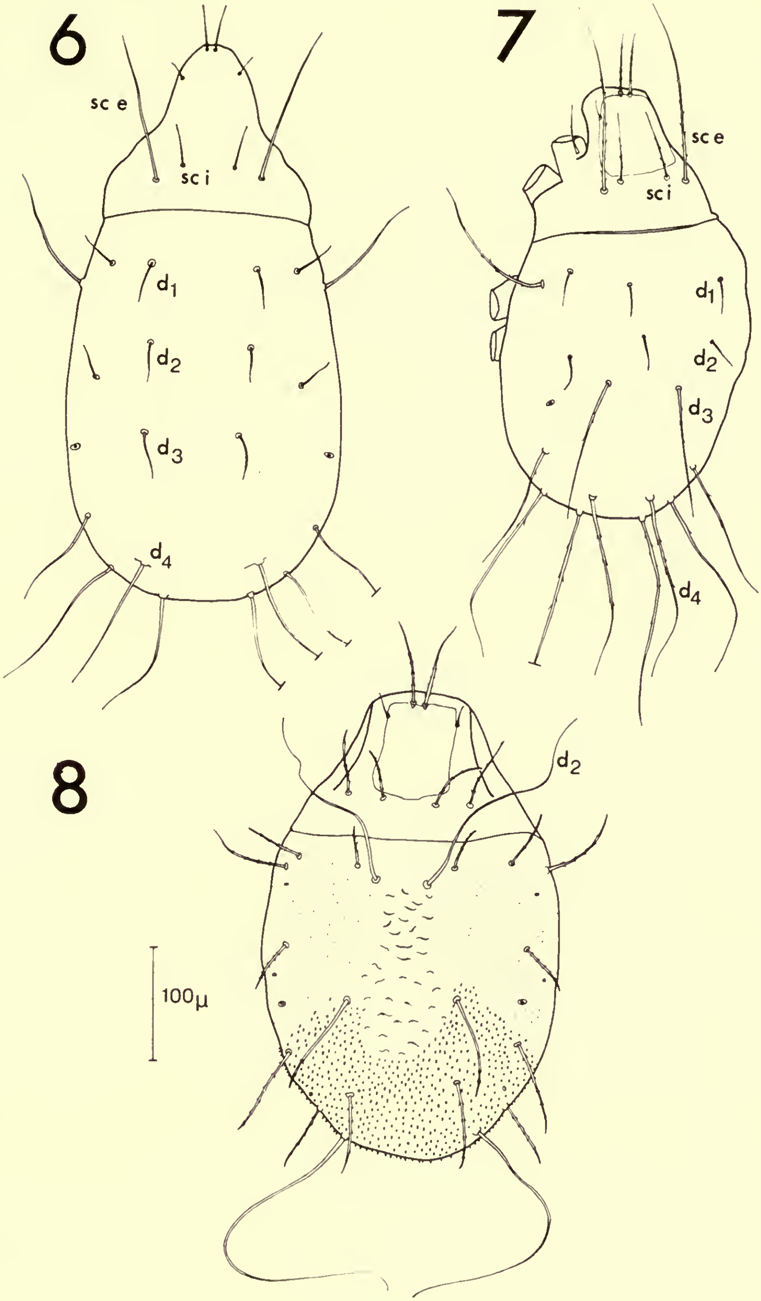


FIG. 5. *Acarus macrocoryne sp.n.* Idiosoma of ♀♀'s taken from a natural population showing range of variation in length of dorsal setae (d_1 to d_4).

Prior to this publication, genu I of *Acarus* males was said to bear two large and one small process and, ventrally, femur I extended into a strong conical spur (Text-fig. 11). The new species described here include one in which the genu bears a single large process sometimes subtended by a much smaller one and another species in which the genual processes are completely lost with the femoral spur considerably reduced in size. I have also seen a single *A. immobilis* specimen in which there is only one large genual process, similar to the condition occurring in *A. macrocoryne*.

It is hoped that the above discussion on morphological variation will provide an insight into why certain taxa (some previously described as specimens *incertae sedis*) have been given specific rank whilst others have not. It has been dealt with in some detail because despite the problem of discontinuous variation, I have had to use the characters which exhibit this phenomenon in order to provide a key to species. Therefore, identifications based on single specimen samples, or samples not properly prepared for microscopic examination, may not be reliable. It is perhaps heartening that the five known hypopal forms are easily distinguishable.


6
sc e
sc i
d1
d2
d3
d4
7
sc e
sc i
d1
d2
d3
d4
8
d2
100μ

FIGS. 6, 7, 8. 6, *Acarus mirabilis* Volgin. ♀. Dorsum of idiosoma; external scapular setae *sc e*; internal scapular setae *sc i*; dorsal setae d_1 to d_4. Re-drawn after Volgin (1965). 7, *Acarus tyrophagoides* (Zachvatkin) ♀. Dorso-lateral view idiosoma. 8, *Acarus gracilis* Hughes ♀. Dorsum of idiosoma.

4. PREPARATION OF MATERIAL FOR MICROSCOPIC EXAMINATION

Before making a permanent mount, the specimens require to be cleared. Add two or three specimens to a drop of 70 per cent lactic acid and cover with a number 0, one cm diam. cover-slip. Place on a slide-warmer or in an oven at 50–60°C for one or two days.

Before making a permanent preparation, the lactic acid should be neutralised by placing the cleared specimens in a drop of Vitzthum's fluid* for up to one hour or more. This can best be achieved by surrounding the cover-slip of the temporary lactic acid mount with Vitzthum's fluid, using the fluid to float off the cover-slip. The specimens can then be pushed to a clean spot of fluid with the tip of a very fine needle. Finally, remove to a clean slide and mount in Berlese's fluid.

If more than one specimen is available, some should be mounted in a dorso-ventral position, others should be manoeuvred so that solenidion ω_1 on tarsus II can be viewed laterally. One specimen per slide under a small cover-slip is preferable. The key to adults is based on material prepared as above and examined by means of phase-contrast microscopy. An oil-immersion objective of high power is required in order to assess the degree of pectination of hysterosomal setae.

5. KEY TO ADULTS AND DESCRIPTION OF SPECIES

(i) KEY TO ADULTS

1 External scapular setae (*sc e*) more than twice as long as internals (*sc i*), e.g. Text-fig. 6. 2

– External scapulars about equal in length to internal pair, e.g. Text-fig. 10. . . 3

2 Seta d_3 long, equal or almost equal in length to d_4 and at least three times as long as d_1 or d_2 which are short (Text-fig. 7). Solenidion ω_1 with a stout shaft and distinct terminal head. . . . . ***A. tyrophagoides.***

– Seta d_3 short, about equal in length to d_1 and d_2, so that all three are much shorter than d_4 (Text-fig. 6). . . . . ***A. mirabilis.***

3 Dorsal setae d_2 four to five times longer than d_1 and twice length of d_3 (Text-fig. 8). Solenidion ω_1 usually slender, always tapering towards the apex (Pl. I, fig. 3) . . . . ***A. gracilis.***

– Length of d_2 intermediate between length of d_1 and d_3, never more than three times longer than d_1 and at most a little longer than d_3 4

4 Ventral distal spine *s* of tarsus I and II (not tarsus I of ♂) large, about equal in length to length of tarsal claw; ventro-posterior margin concave, claw tip directed backwards (Pl. IV, fig. 1). Solenidion ω_1 recumbent with distinct 'goose-neck' before terminal expansion (Pl. I, fig. 4). Usually, dorsal setae are short (see p. 89). . . . . ***A. siro s. str.***

– Ventral distal spine *s* slender, about half length of tarsal claw; ventro-posterior margin of claw convex, claw tip directed forwards (Pl. IV, fig. 2) 5

5 Hysterosomal setae *hi, la, lp* and dorsals d_1 to d_4 short. In particular, the length of dorsal seta d_2 or d_3 does not exceed the distance between its base and base of the dorsal seta immediately posterior to it. (e.g. Text-figs. 2a and b). 6

– Hysterosomal setae *hi, la, lp* and dorsals longer; generally, in the majority of individuals of a given population, the length of d_2 and d_3 is greater than distance between its base and base of the seta immediately posterior to it (e.g. Text-fig. 15). (See p. 90 for details of setal length variation) 8

6 Solenidion ω_1 with sides almost parallel, expanding into a distinct egg-shaped terminal head which at widest part is wider than widest portion of stem (Pl. I, figs. 1 & 2).

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* Chloral hydrate 50g, Phenol 45g, Distilled water 5cc.

Femoral spur and genual processes on leg I of ♂ normal (e.g. Text-fig. 11). ***A. immobilis.***

– Solenidion ω_1 without distinct egg-shaped terminal head: ♂ leg I normal or with reduced spur and genual processes absent 7

7 Male leg I with normal spur and two tooth-like genual processes (Text-fig. 11)*. Solenidion ω_1 short, compact, with sides expanding gradually from the base then narrowing to an indistinct neck before expanding into a terminal head. Width of widest part of head equal to width of widest portion of stem (Pl. II, fig. 1). ***A. farris***

– Male leg I with femoral spur much reduced so that seta *vF* arises almost at spur apex; genual processes absent. (Text-figs. 33 & 35). Solenidion ω_1 much more slender, with a distinct neck in distal half (Pl. II, fig. 2). . ***A. calcarabellus sp.n.***, p. 107

8 Scapular setae with one or at most two pectinations, hysterosomal setae smooth†, long (especially those of opisthosoma) terminating in fine whip-like endings (Text-figs. 27 & 28). Solenidion ω_1 short with parallel sides (Pl. III, fig. 2). . . . . ***A. chaetoxysilos sp.n.***, p. 105

– Scapular setae strongly pectinate; hysterosomal setae with varying degrees of pectination but some opisthosomal setae *always* pectinate 9

9 Hysterosomal setae d_2, d_3, *sa i* and *sa e* strongly pectinate; also pectinations usually but not always present on *hi*, d_1, *la* and *lp*. 10

– Setae d_2 and d_3 smooth as are *hi*, d_1 and *la*; setae *lp* and *sa i* may also be smooth . 11

10 Solenidion ω_1 large, expanding gradually from the base into a large swollen tip; the whole solenidion slightly curved (Pl. II, fig. 4). Male with normal femoral spur and a single large tooth-like process on genu I (Text-figs. 22–24). . . . . ***A. macrocoryne sp.n.***, p. 102

– Solenidion ω_1 short and thick, as thick as or thicker than basal portion of solenidion psi of tibia; sides parallel with an indistinct terminal head (Pl. II, fig. 3). Male genual processes normal in British populations (Text-fig. 11); known from one specimen from U.S.A. in which genu I bears a single tooth (Text-fig. 12). . . . . ***A. nidicolous sp.n.***, p. 93

11 Hysterosomal setae of ♀ including sacrals are smooth (Text-fig. 39). ♂ sacrals sparsely pectinate but remainder of hysterosomal setae are smooth. Supra-coxal seta long, tenuous and sparsely pectinate (Text-fig. 39). Solenidion ω_1 short, strong, terminating in an egg-shaped head, with convexity of one side more distinct (Pl. III, fig. 3). . . . . . Specimen ***incertae sedis*** ex cocoanuts, Brazil, p. 110

– Both sexes with opisthosomal setae *lp*, d_4 and sacrals pectinate. Supra-coxal seta long and strongly pectinate 12

12 Solenidion ω_1 with a slender shaft terminating in an obvious egg-shaped head. (Text-fig. 38 and Pl. III, fig. 4). . . . . Specimen ***incertae sedis*** ex citrus fruit, Formosa, p. 109

– Solenidion ω_1 short, with a thick shaft terminating in an egg-shaped head (Pl. III, fig. 1). . . . . Specimen ***incertae sedis*** ex water-chestnuts, China, p. 112

(ii) ***Acarus nidicolous*** sp.n

The gross morphology resembles that of the adults of the *Acarus siro* complex (Griffiths, 1964) and, in the main, only the differences are discussed below.

MALE. Length of idiosoma of five males, reared on a wheat germ and yeast mixture at 90 per cent relative humidity and 20°C, = 0·365 mm average. Idiosomal measurements were taken from the centre of an imaginary line connecting anterior tips of epimeron fork to the centre of the posterior margin of the body.

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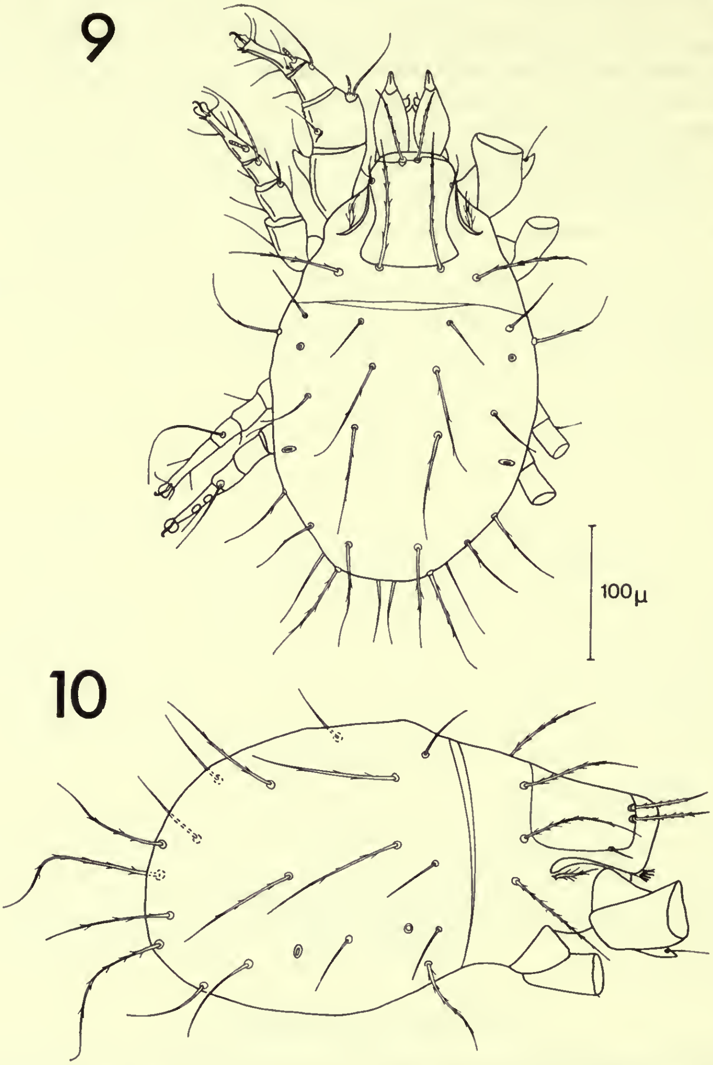
* The two species in couplet 7 are easily separated on secondary sexual characters on leg I of the ♂. In the absence of ♂♂'s, identification is based on shape of solenidion ω_1 on tarsus II, viewed laterally and is more difficult. *A. calcarabellus* is very rare.

† Should be examined under oil-immersion phase-contrast microscopy.

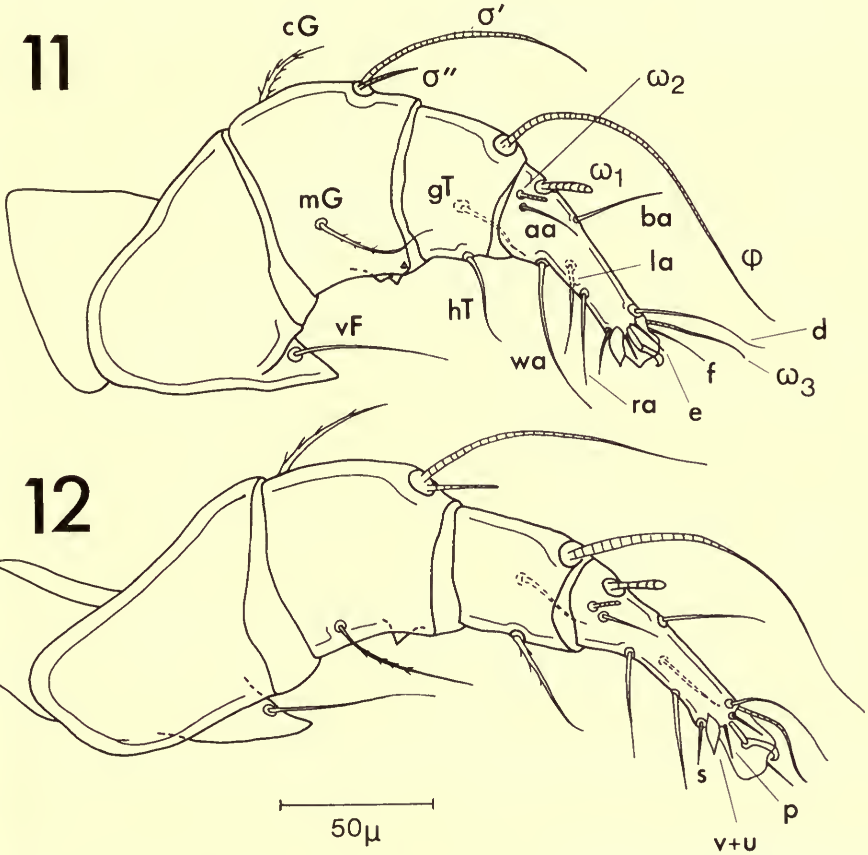
(i) *Dorsum* : (Text-fig. 9). Number and distribution of setae on dorsum and venter



Figs. 9, 10, 9, *Acarus nidicolous sp.n.* ♂. Idiosoma, dorsum. Specimen collected in Britain. 10, *Acarus nidicolous sp.n.* ♂. Idiosoma, dorso-lateral view. Unique specimen from U.S.A.

same as for *A. siro* complex, but degree of pectination different in that all hysterosomal setae are pectinate or, occasionally d_1, *hi* and sometimes *la* may be smooth.

Length of dorsal idiosomal setae expressed as a percentage of idiosomal length (average of 5 individuals) are as follows: *vi*—17·2%, *ve*—4·9% *sc i*—29%, *sc e*—26%, *hi*—10·9%, *he*—23·3%, *la*—10·1%, d_1—8·6%, d_2—23·7%, d_3—24·6%, d_4—19·2%, *lp*—16·0%, *sa e*—13·5%, *sa i*—31·4%. Thus, with the exception of *sa i*, the dorsal hysterosomal setae are longer than corresponding setae in the *Acarus siro* complex. In particular, d_2 and d_3 are over 20 per cent of the idiosomal length, so that when directed backwards in a straight line, the tips of d_2 extend beyond bases of d_3 and tips of d_3 extend just beyond or level with bases of d_4.

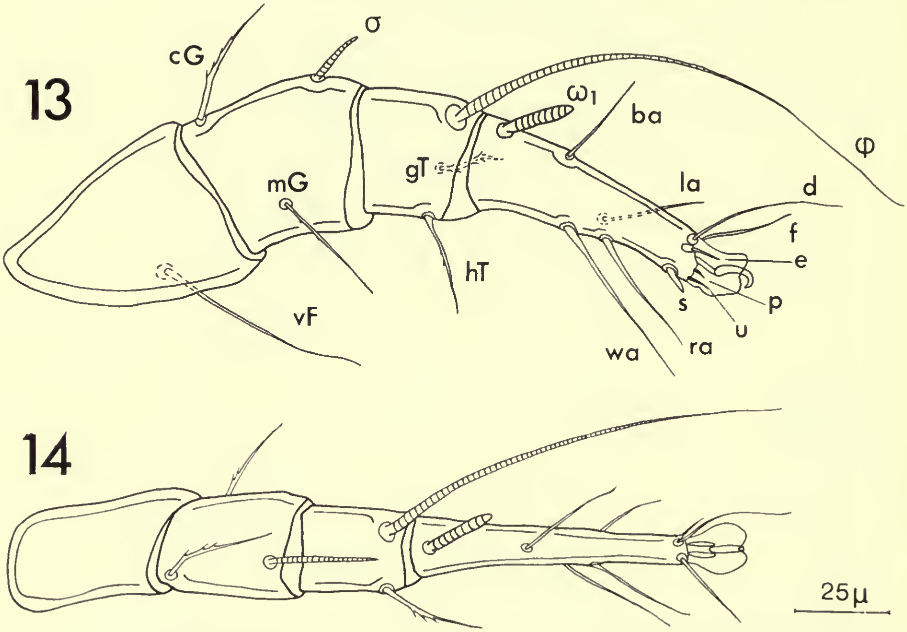


FIGS. 11, 12. 11, *Acarus nidicolous sp.n.* ♂. Leg I, post-axial face; structures labelled ω, σ and φ = solenidia; ε = famulus; remainder (e.g. *aa, e, gT*) = setae. 12, *Acarus nidicolous sp.n.* ♂. Leg I, post-axial face. Unique specimen from U.S.A.

Propodosomal shield similar in shape to that of *A. farris*. Grandjeans' organs, supra-coxal setae, not significantly different in shape from corresponding organs in *A. siro* complex. Electron scanning micrographs showing the structure of Grandjeans' organ and the supra-coxal seta of *A. siro* appear in Pl. IV, figs. 3 and 4, respectively.

(ii) *Venter:* Closely resembles ventral surface of males of the *A. siro* complex. Same complement of setae, smooth or at most with one or two pectinations. Position of post-anal setae relative to anal opening as for *A. siro* complex; their lengths relative to each other also similar. No significant difference in structure of genitalia or apodemes.

(iii) *Legs*: I & II. Five segmented with well developed pre-tarsus terminating in a stalked claw. Genu and femur of leg I of ♂ much enlarged, femoral apophysis and genual projections as found in *A. siro* complex (Text-fig. 11). The chaetotaxy of leg II and the shape of solenidion ω_1 is described in Text-fig. 12. A micrograph of ω_1 on leg II is also shown in Plate II, fig. 3. In shape, it is relatively short, thick, and " cigar-shaped ". Throughout its whole length it is thicker than the basal section of solenidion psi of the tibia.



FIGS. 13, 14. 13, *Acarus nidicolous sp.n.* ♂. Leg II. 14, *Acarus nidicolous sp.n.* ♂. Leg II. Unique specimen from U.S.A.

(iv) *Morphological variation*:

Dr. Dean Furman presented me with a single ♂ specimen taken from the nest of *Neotoma fuscipes*, Wildcat Canyon, Alamada Co., California, U.S.A., June 1964. The length of the idiosomal setae of this specimen appears to be the same as for British males of *A. nidicolous* (compare Text-fig. 9 with 10). However, genu I bears only one large process instead of the usual two large and one small process (compare Text-fig. 11 with 12). These same figures illustrate that seta *hT* of leg I is smooth in British males but pectinate on the North American specimen. Also on genu II solenidion sigma of the North American specimen is much longer (compare Text-fig. 13 with 14).

Until further material can be obtained from the south-western areas of the United States, this specimen must be considered a variant of *A. nidicolous*.

FEMALE (Text-fig. 15). Body larger and more roundly oval than male.

(i) *Dorsum* : As for male, except that propodosomal setae, expressed as percentage of idiosomal length are slightly shorter, whereas the hysterosomal setae are longer, except *sa i* which is about the same in both sexes. The average lengths of idiosomal setae (from 5 females) are as follows:
vi—14·9%, *ve*—4·0%, *sc i*—24·5%, *sc e*—23·3%, *hi*—13·3%, *he*—24%, *la*—15·2%, *d*1—11·6%, *d*2—25·2%, *d*3—27·4%, *d*4—23·3%, *lp*—22·3%, *sa e*—22·3%, *sa i*—31·0%.

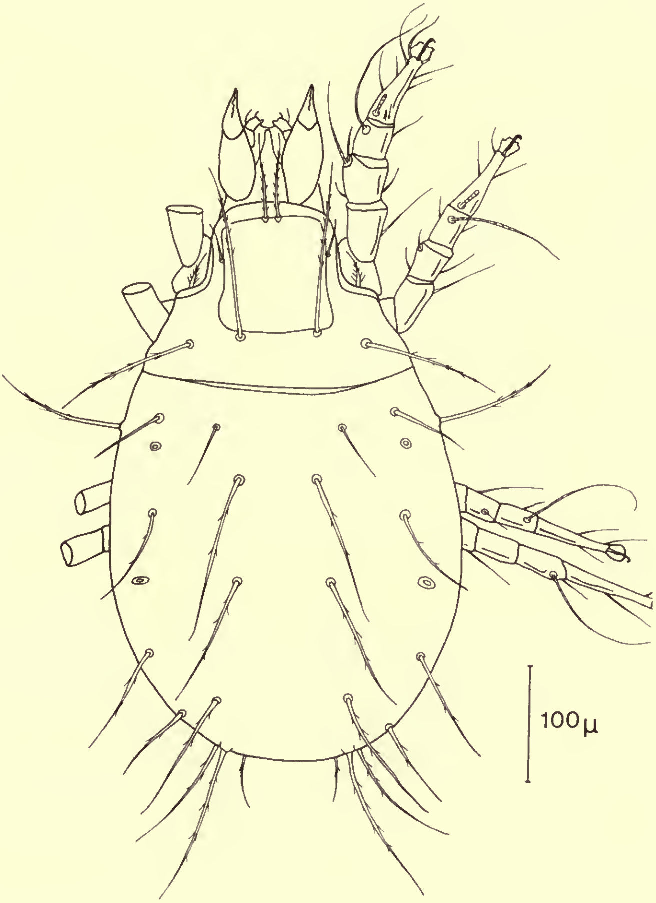


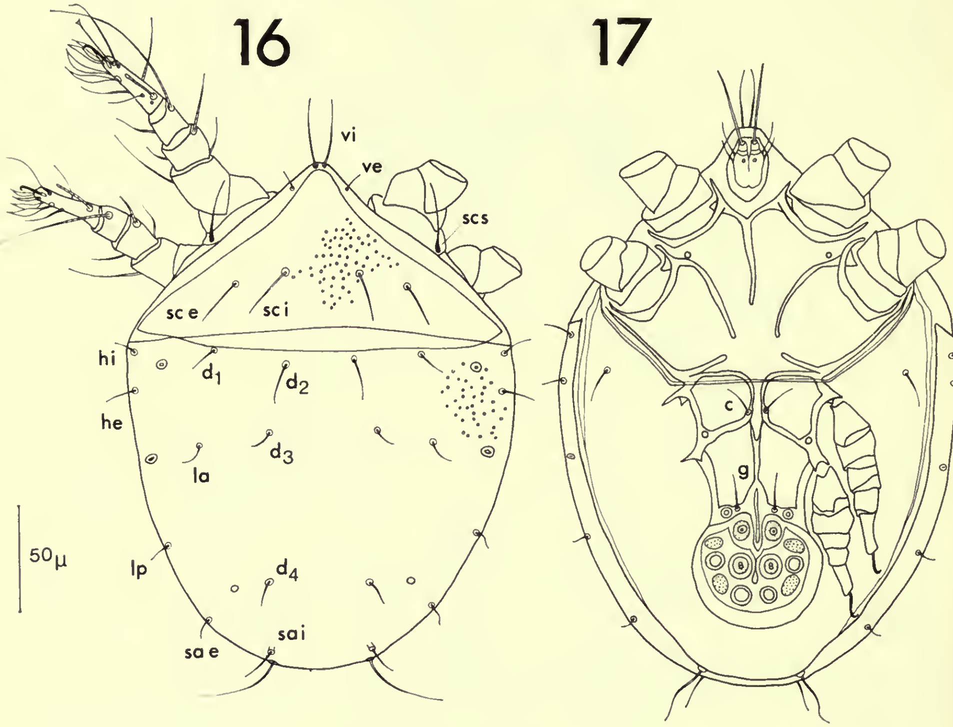
FIG. 15. *Acarus nidicolous sp.n.* ♀. Dorsum.

(ii) *Venter* : Morphology same as for *A. siro* complex females. Length of anal and post-anal setae, relative to each other, is very similar to that in *A. siro sensu stricto*.

(iii) *Legs* : Leg chaetotaxy and shape of solenidion ω_1 as for male.

HYPOPUS (Text-figs. 16 to 21). Colour of live specimens pinkish-beige. Gross morphology the same as that of motile hypopi of the *A. siro* complex. Only the differences are given below.

(i) *Dorsum* (Text-figs. 16) : Surface punctations smaller and not so dense. Setae *ve* almost smooth compared with dense pectinations of the same setae in the *Acarus siro* complex. All idiosomal setae are short, narrow and finely pointed. In particular, the four scapular setae (*sc i* and *sc e*) do not extend beyond posterior margin of the propodosomal shield. On extreme posterior margin a pair of setae, possibly homologous with *pa* are the longest pair on the hysterosoma.



FIGS. 16, 17. *Acarus nidicolous sp.n.* Hypopus. 16, Dorsum. 17, Venter.

(ii) *Venter* (Text-fig. 17) : On gnathosoma, at base of each lobe which bears an arista, there is a small clear circular area which is not found in other motile *Acarus* hypopi.

Coxal skeleton much more defined. In freshly mounted specimens coxal fields III and IV can be seen to be enclosed. However, in older, permanent mounts those parts of the coxal skeleton which join apodemes III and IV and divide coxal fields IV fade, so that coxal fields III and IV may appear to be open. I have recently discovered that this phenomenon is true for other *Acarus* motile hypopi. Thus, the character " closed or open coxal fields " is not a reliable one to use in a taxonomic key.

The pair of genital setae (*g*) arise on a level with the anterior margin of the pairs of suckers which outflank them.

(iii) *Legs* : The four apical segments of legs I to IV are described in Text-figures 18 to 21.

LEG CHAETOTAXY OF ALL STAGES. Nomenclature follows Grandjean (1939).

The numbers of setae and solenidia on each segment of each leg of all stages is given below as a formula. The famulus (ε), which is present immediately in front of ω_1 on tarsus I in all stages is not included in the formula. The five groups of figures inside each parentheses represent, from left to right, tarsus, tibia, genu, femur and trochanter.

Setae

	Leg I	II	III	IV
Larva	(13.2.2.1.0.)	(12.2.2.1.0.)	(10.1.1.0.0.)	(–)
Protonymph	(13.2.2.1.0.)	(12.2.2.1.0.)	(10.1.1.0.0.)	(8.0.0.0.0.)
Hypopus	(9.2.2.1.0.)	(9.2.2.1.0.)	(8.1.1.0.1.)	(8.1.0.1.0.)
Tritonymph	(13.2.2.1.1.)	(12.2.2.1.1.)	(10.1.1.0.1.)	(10.1.0.1.0.)
Adult	(13.2.2.1.1.)	(12.2.2.1.1.)	(10.1.1.0.1.)	(10.1.0.1.0.)

Solenidia

	Leg I	II	III	IV
Larva	(1.1.2.0.0.)	(1.1.1.0.0.)	(0.1.1.0.0.)	(–)
Protonymph	(2.1.2.0.0.)	(1.1.1.0.0.)	(0.1.1.0.0.)	(0.0.0.0.0.)
Hypopus	(2.1.1.0.0.)	(1.1.1.0.0.)	(0.1.0.0.0.)	(0.1.0.0.0.)
Tritonymph	(3.1.2.0.0.)	(1.1.1.0.0.)	(0.1.1.0.0.)	(0.1.0.0.0.)
Adult	(3.1.2.0.0.)	(1.1.1.0.0.)	(0.1.1.0.0.)	(0.1.0.0.0.)

The chaetotactic formula for *A. farris* given in Griffiths (1964) should be amended to agree with the above. This involves three alterations, namely:

(a) Protonymph setae, leg IV, tarsus I—replace figure 7 with an 8. I am now satisfied that spine *s* is present as a minute structure.

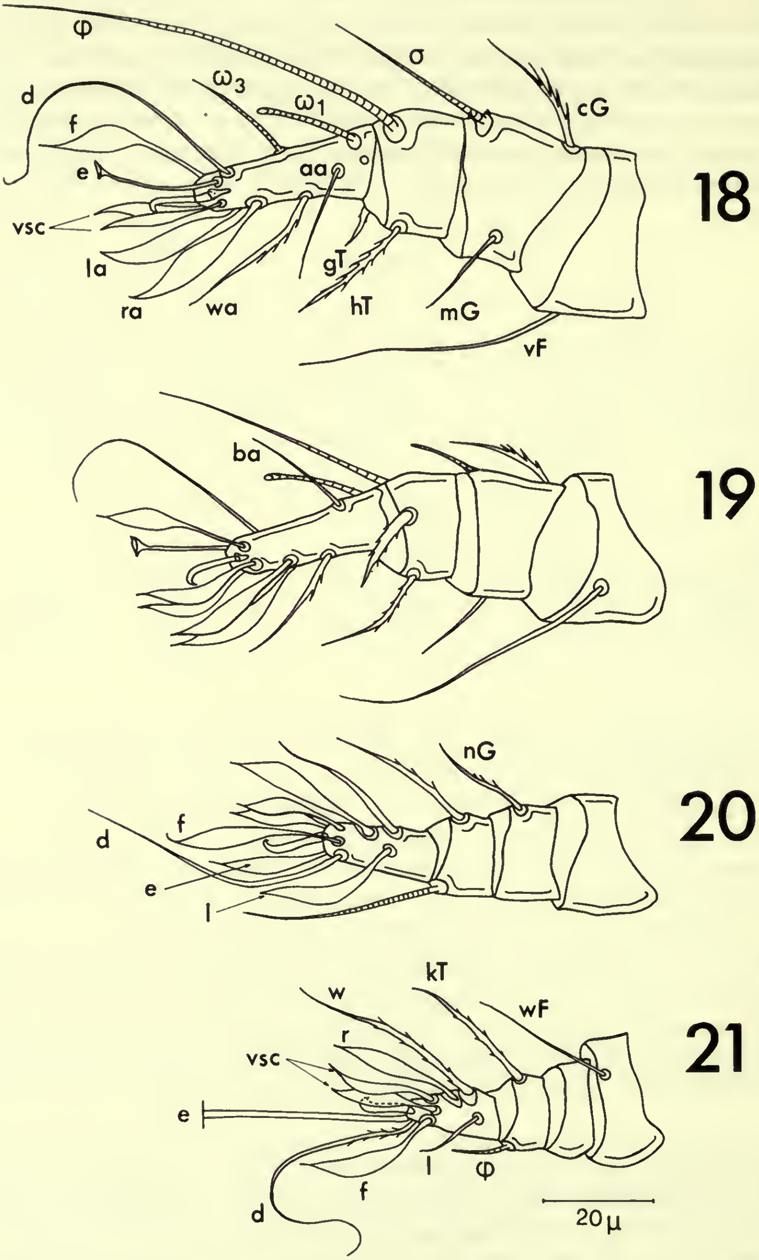
(b) Hypopal seta, leg I, tarsus I—replace figure 10 with a 9. Seta *ba* is NOT present.

(c) Hypopal solenidia, leg I, tarsus I—replace figure 1 with a 2. Solenidion ω_3 is present. In Griffiths (1964) it was mistakenly termed seta *ba*.

When the above corrections are taken into account, the chaetotactic formula for this species is identical with the formula for those species of the *A. siro* complex which have a motile hypopus. Also, the position of the respective setae and solenidia and, in general, their length and the degree of pectination of the setae are remarkably similar. However, as already mentioned, in adult specimens the shape of ω_1 is distinct.

BIOLOGY AND HYBRIDIZATION EXPERIMENTS. This species has been reared successfully in the laboratory for a period of four years. Single pair matings of virgin adults have been made to determine egg output and hatch. The pairs were reared in individual cells under the same physical conditions as the stock cultures namely, 20°C and 90 per cent relative humidity, with dried yeast powder as food.

Twenty-five pairs laid 2044 eggs over a 15 day period. Maximum for any one pair


φ
ω3
ω1
σ
d
f
e
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cG
vsc
la
ra
wa
gT
hT
mG
vF
18
ba
19
nG
d
f
e
l
20
kT
w
wF
r
vsc
e
l
φ
f
d
21
20μ

FIGS. 18–21. *Acarus nidicolous sp.n.* Hypopal leg chaetotaxy (excluding trochanter segment). 18, left leg I. 19, left leg II. 20, left leg III. 21, left leg IV.

was 137 and minimum 40, with an average per pair of 82. Percentage hatch was 85·9%.

The same technique as described above has been employed to cross *A. nidicolous* with the three species of the *A. siro* complex. Twenty initial crosses, in *each* direction were completed. Viable eggs were obtained only from the cross *A. immobilis* ♂ × *A. nidicolous* ♀. The results (Table 1) show that only 4 pairs produced eggs and indicate the presence of a reproductive isolating mechanism at the gamete level since each fertile pair produced very few offspring. With these offspring, 10 F_1 sibling and non-sibling crosses were performed. Seven crosses produced small numbers of eggs but none hatched.

TABLE 1

Details of the four viable interspecific crosses
A. immobilis ♂ + *A. nidicolous* ♀

Pair number	Number of eggs per cross	% hatch	No. of offspring reaching maturity*	
			♀♀'s	♂♂'s
1	76	47·3	4	1
2	58	29.9	11	5
3	45	13·3	2	2
4	85	21.1	0	8

* F_1 crosses made with these adults failed to produce an F_2 generation.

DISTRIBUTION, HABITAT AND LOCALITY. Known from animal nests in Great Britain, namely; in unidentified small rodent nest, grounds of Pest Infestation Lab., Slough, Bucks., March 1964; breeding nest of hedgehog (*Erinaceus europaeus* L.), Pest Infestation Lab., Slough, Bucks., April 1964; squirrel drey, (*Sciurus carolinensis*), Wytham, near Oxford, April 1964; nest of hooded crow (*Corvus cornix*), Eileen mor, Inverpolly, Scotland, June 1964; mole (*Talpa europaea* L.) breeding nest, Foxfield, Wilts., January 1964; mole nest, Sittard. December 1911. Also from cheddar cheese, Slough, Bucks., 1967.

One ♂ from nest of *Neotoma fuscipes*, California, U.S.A., has also been assigned to this species (see p. 96).

MATERIAL DEPOSITED IN NATIONAL MUSEUMS

(i) British Museum (Natural History).

HOLOTYPE : ♂. England, Bucks., Slough; nest of unidentified small mammal in grass bank; March, 1964. Coll. D. A. Griffiths. BM(NH) registration number 1969.38

PARATYPES : Three ♂♂s, 6♀♀ and 3 hypopi, on 11 slides. BM(NM) registration numbers 1969.39 to 1969.41 inclusive. Data as for holotype.

OTHER MATERIAL : Three ♂♂, 1 ♀, 16 hypopi, on 5 slides. England, Oxfordshire, Wytham woods; *Sciurus carolinensis* nest (Grey squirrel's drey); April, 1964. Coll.

D. A. Griffiths. BM(NH) reg. numbers 1969.44 and 45 inclusive. One ♀, Scotland. Eileen mor, Inverpolly; *Corvus cornix* nest; June, 1964. Coll. G. E. Woodroffe. BM(NH) reg. number 1969.46.
One ♂, 2 hypopi, on 2 slides. England, Wilts., Foxfield; *Talpa europaea* breeding nest; Jan., 1964. BM(NH) reg. numbers 1969.47 and 48.
One ♀, 1 hypopus, on 2 slides. England, Bucks., Slough; *Erinaceus europaens* breeding nest, April 1964. Coll. D. A. Griffiths. BM(NH) reg. numbers 1969.42 and 43.

(ii) United States National Museum (Washington).

PARATYPES : Four ♂♂, 6 ♀♀ and 3 hypopi, on 8 slides. Data as for holotype.

OTHER MATERIAL : USA, California, Alameda Co., Wildcat Canyon; *Neotoma fuscipes* nest, June 1st, 1964. Collrs. Chaniotis & Stumpf.

(iii) Institute of Acarology, Wooster, Ohio, U.S.A.

PARATYPES : Four ♂♂'s, 3 ♀♀ and 2 hypopi, on 7 slides. Data as for holotype.

(iv) Rijksmuseum van Naturlijke Historie, Leiden, Holland.

OTHER MATERIAL : One slide bearing eleven hypopi. For data see item 2, page 114.

(iii) ***Acarus macrocoryne*** *sp.n.*

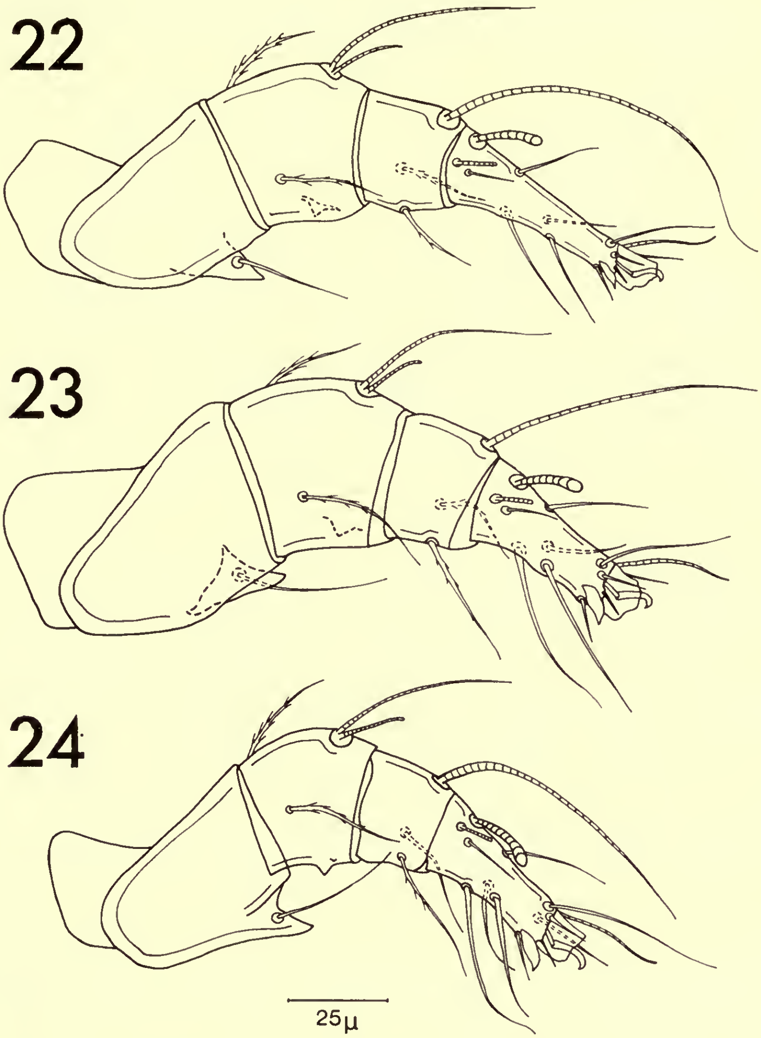
Previously, (Griffiths, 1964, p. 456), I referred this taxon to the category 'specimens *incertae sedis*'. The species is represented by two populations collected near Santa Fé, New Mexico, U.S.A. in 1952 and 1953. They were taken from two separate but similar habitats namely, the nests of the small mammals *Perognathus flavus* and *Dipodomys spectabilis*.

The mites from the *P. flavus* nest (36 specimens on one slide) are all very small and have short tarsi. The material from the *D. spectabilis* nest consists of specimens with similar short cylindrical tarsi together with others in which the tarsi are much longer, tapering towards the extremity (Text-figures 22, 23 and 24). Hysterosomal setae, *sc e*, d_2, d_3 and *lp* of long tarsi specimens also tend to be longer than the corresponding setae in the respective sexes of short tarsi specimens. The extremes of variation in length of hysterosomal setae shown by this population is illustrated in Text-fig. 5.

Since it has been shown (Griffiths, 1966) that tarsal length and shape can be influenced by varying the nutritional value of the food given to pre-adult stages, and because Text-figures 2 and 3 show that similar variations in setal lengths occur in *Acarus siro sensu stricto*, it is considered that the forms within the *D. spectabilis* nest population represent intraspecific variation.

MALE AND FEMALE (Text-figures 22 to 26 inclusive). Distribution and number of setae on the idiosoma is normal. Setae *he*, d_1 and *la* appear to be smooth in some " short tarsi " specimens, remainder are pectinate. Setae of " long tarsi " specimens with slightly more pectinations than " short tarsi " specimens. Because of the variation in length exhibited by the dorsal setae of the idiosoma, the lengths of these setae relative to body length is not given, but are adequately illustrated in the accompanying text-figures. In general, the lengths of the dorsal setae d_2, d_3 and d_4

may be used with discretion to distinguish this species from members of the *A. siro* complex. Where populations are represented by single specimens or a few individuals this character may not in itself be conclusive.

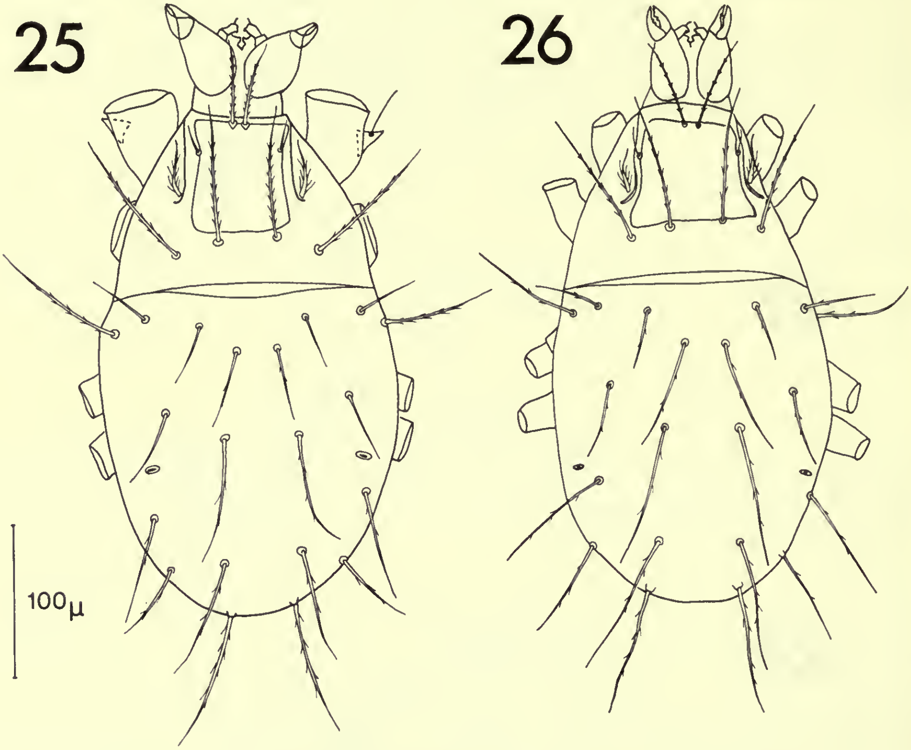


Figs. 22–24. *Acarus macrocoryne sp.n.* Leg I chaetotaxy and tarsal length variation. 22, a " long tarsus " specimen ex *D. spectabilis* nest. 23, a " short tarsus " specimen from the same population. 24, leg I of specimen from a population found in the nest of *Perognathus flavus*. The whole population has very short tarsi.

Remaining features of the idiosoma not significantly different from those of the *A. siro* complex.

Genu and femur of leg I of the male much enlarged as usual but the projections on the genu are reduced to one large tooth and sometimes a minute sub-tending tooth, compared with the two large and one small projection found on genu I of the males of *Acarus* species described previously.

LEG CHAETOTAXY (Text-figures 22 to 24). Position, length and, where applicable, the degree of pectination of setae not significantly different from that described for the *A. siro* complex.



FIGS. 25, 26. *Acarus macrocoryne sp.n.* dorsum. 25, ♂. 26, ♀.

Solenidion ω_1 on tarsus I and II is long, slightly curved, expanding towards the apex into a distinct head. The internal margin of the head is more expanded than the external margin (Pl. II, Fig. 4).

The famulus is minute and difficult to discern even under oil-immersion phase-contrast microscopy.

MATERIAL DEPOSITED IN NATIONAL MUSEUMS.

(i) United States, Washington.

HOLOTYPE : on slide with data as given below I select the male specimen which bears long setae. The position of the holotype specimen is indicated by a labelled diagram attached to the slide. It is the second specimen in from the right-hand edge of the cover-slip as viewed through a stereoscopic binocular microscope and the second from the left as viewed through a compound microscope. There are another 3 ♂♂ and a nymph on the slide, these 4 specimens constitute paratypes.

Data : USA, New Mexico, Santa Fé; *Dipodomys spectabilis* nest 63A ; Feb. 2nd, 1953. Coll. H. B. Morlan.

PARATYPES : Three ♀♀ on one slide, with same data as for holotype.

Twenty ♂♂s and 16 ♀♀s, on one slide. USA, New Mexico, Santa Fe; *Perognathus flavus* nest ; Feb. 29, 1952. Coll. H. B. Morlan. USNM reg. number Lot 52-11181.

(ii) British Museum (Nat. Hist.)

PARATYPES : Single ♂ and 2 ♀♀, on 2 slides. Data as for holotype. BM(NH) reg. numbers 1969.51 and 52.

(iv) ***Acarus chaetoxysilos*** sp.n.

In Griffiths, 1964 this taxon was not given specific rank because at the time it was known from two specimens only. These were imported into the United States of America from Japan on *Citrus* sp. More recently, in a collection of *Acarus* material kindly loaned by Dr. D. E. Johnston, Institute of Acarology, Ohio, U.S.A., I found another male which was also introduced from Japan into the U.S.A. But, on this occasion, the cargo was " Irish " potatoes and the time interval separating the two collections is twelve years.

MALE AND FEMALE

(i) *Idiosoma* (Text-figures 27, 28). General body conformation same as that described for other *Acarus* species. Genu I of male bears two strong teeth and one smaller projection as in *A. nidicolous*. Spine *s* angled forward and about half length of tarsal claw. (See pl. IV, fig. 2 for example.)

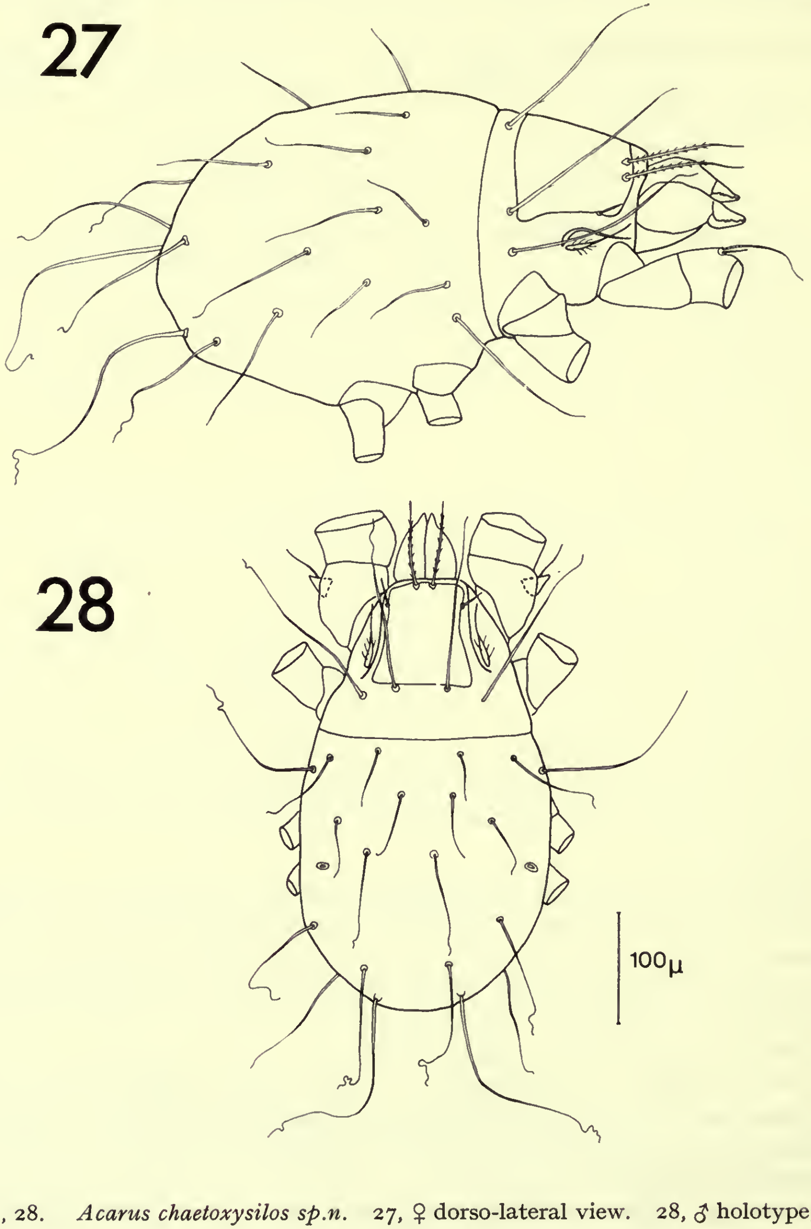
On the idiosoma the vertical internal setae (*vi*) are pectinate but, except for a single pectination on some of the scapular setae, the remaining setae are smooth, long and whip-like, tapering so finely towards their tips that only when viewed by oil-immersion phase-contrast equipment can their full length be seen. Setae *hi* and all setae of the dorsum posterior to d_2 are exceptionally long, resembling the posterior train of setae of *A. tyrophagoides* but different from this species because the internal scapulars (*sa i*) are long. The terminal portion of the supra-coxal seta is also extended into a fine tapering thread.

(ii) *Legs* (Text-figures 29, 30). The glabrous setae of the tarsi are also long with fine whip-like endings. Setae of the tibia and genu are pectinate as for other species.

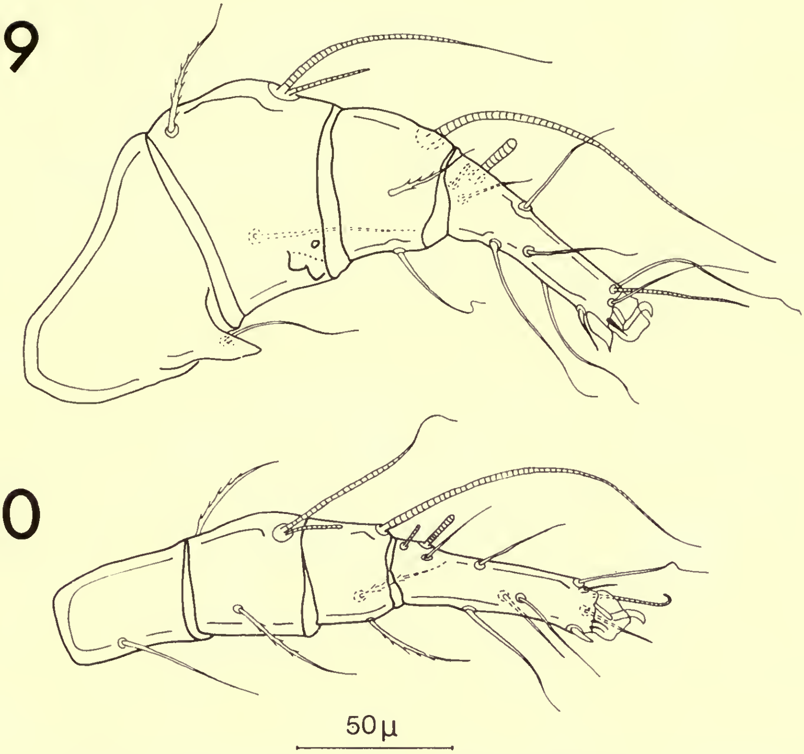
On tarsus I and II ω_1 is fairly short, evenly cylindrical from the base until just before the apex, where it expands almost imperceptibly into a poorly defined head (Pl. III, fig. 2). It is similar in shape to ω_1 of *A. nidicolous*. The trivial name has been derived from *chaeta*, hair; *xysilos*, shaven.

HOLOTYPE : I select as holotype the ♂ specimen on United States National Museum slide number 40.21938. There is one ♀ paratype of the same taxon on the same slide. Data : On *Citrus* sp., Japan, at Seattle, Washington, October 10th, 1940. Seattle No. 9081.

PARATYPES : In addition to the ♀ mentioned above, there is one ♂ (together on same slide with a number of ♀♀ which are not of this taxon) with the following data : " Irish " potatoes, Japan : at Boston, February 28th, 1956; Collr. Lantz & Averill, Lot 56 ; 3105. In the collection of the Institute of Acarology, Columbus, Ohio, U.S.A.



FIGS. 27, 28. *Acarus chaetoxysilos sp.n.* 27, ♀ dorso-lateral view. 28, ♂ holotype, dorsum.



FIGS. 29, 30. *Acarus chaetoxysilos sp.n.* Leg I chaetotaxy (excluding trochanter segment). 29, ♂. 30, ♀.

(v) ***Acarus calcarabellus*** sp.n.

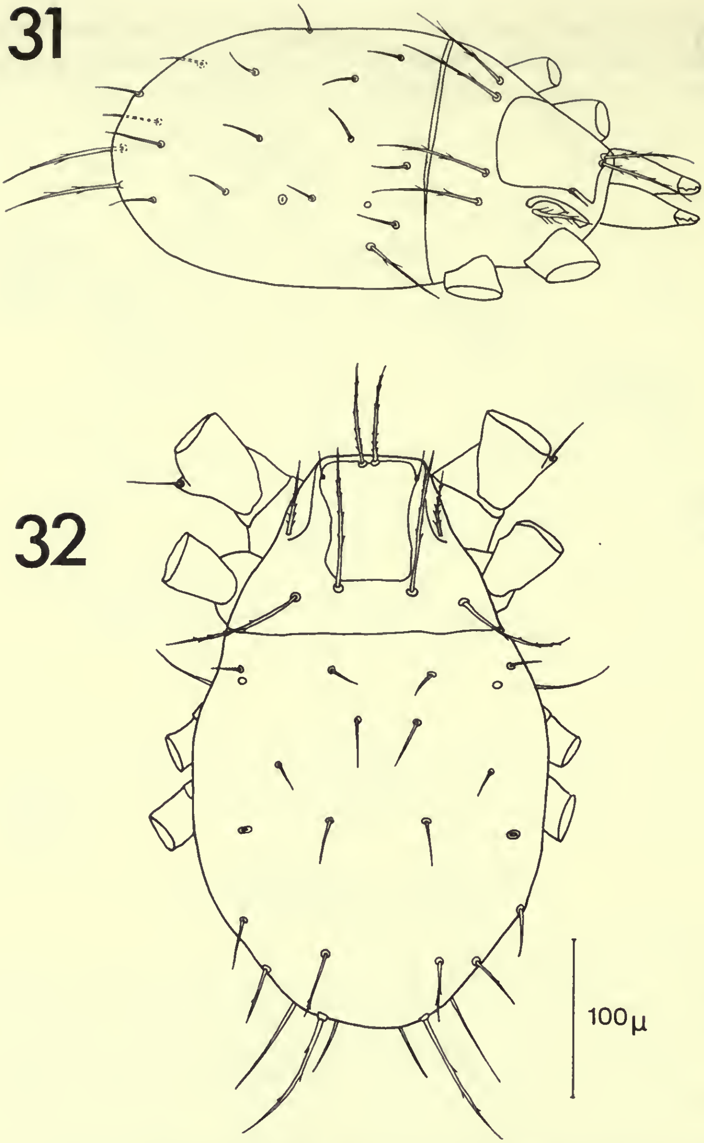
MALE AND FEMALE (Text-figs. 31 to 36).

(i) *Idiosoma.* The general body conformation is the same as that described for other *Acarus* species. However, it should be noted that in all specimens the idiosomal setae are very short and sparsely pectinate (Text-figs. 31 and 32).

(ii) *Legs.* Genu I of ♂ is devoid of all protruberances and the spur on femur I is reduced so that seta *vF* arises very close to the tip of the spur. When viewed from some angles it appears to arise directly from the tip. The structure of genu I and femur I serves to distinguish the male from males of all other known species in the genus (Text-figs. 33 and 35).

The shape of solenidion ω_1 on tarsus I and II in both sexes is distinct (Pl. II, fig. 2). It is relatively long, especially on tarsus II, and a little more slender than ω_1 of previously described species. Well before the apex, it expands slightly to form a long lozenge-shaped club, best observed when the solenidion on tarsus II is viewed laterally.

A population consisting of 3 females and a single male was given to me by Dr. van Eyndhoven, who commented upon the unusual shape of the male spur. I took



Figs. 31, 32. *Acarus calcarabellus sp.n.* ♂. 31, ♂ ex cheese, dorso-lateral view. 32, ♂ ex *Erithracus rubecula* nest.

another small population from the nest of a robin (*Erithacus rubecula*) where it was in association with *A. farris*.

Holotype : ♂. England, Berks., Ascot; *Erithacus rubecula* nest, box no. DAG/70; Feb., 1966. Coll. D. A. Griffiths. BM(NH) reg. number 1969.49.

Paratypes : the following are in my collection ; one slide bearing single ♂, data as for holotype, two ♀♀ and one ♂ on three slides, data—Holland, 1964; ex kaas [cheese].

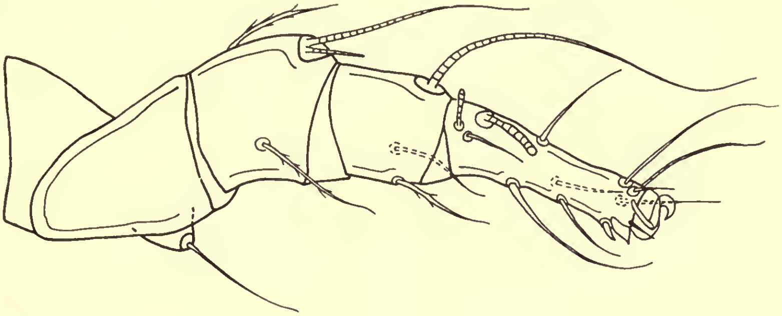
6. SPECIMENS INCERTAE SEDIS

(i) ***Acarus*** population ex *Citrus grandis* fruit, Formosa, imported into U.S.A., Oct. 8th 1956.

This taxon is known from two females and nine nymphs on one slide. Data ; United States National Museum number 56-12672, on *Citrus grandis* fruit, Phila. Pa. October 8th 1956, J. Freedland Colr.

The females are distinguishable from *A. immobilis* only in as much as firstly, the dorsal setae d_2 to d_4 inclusive are longer than the corresponding setae representing the extremes of variation observed in *A. immobilis* (Text-fig. 37). Secondly, solenidion ω_1, although similar in shape to ω_1 of *A. immobilis*, has a much more slender shaft. (Pl. III, fig. 4).

33



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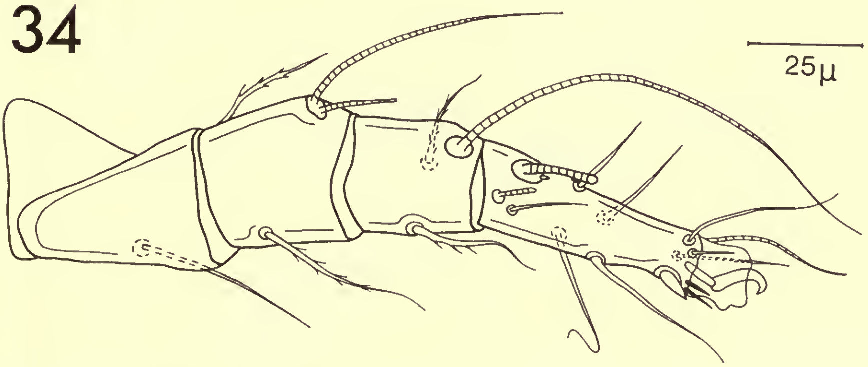
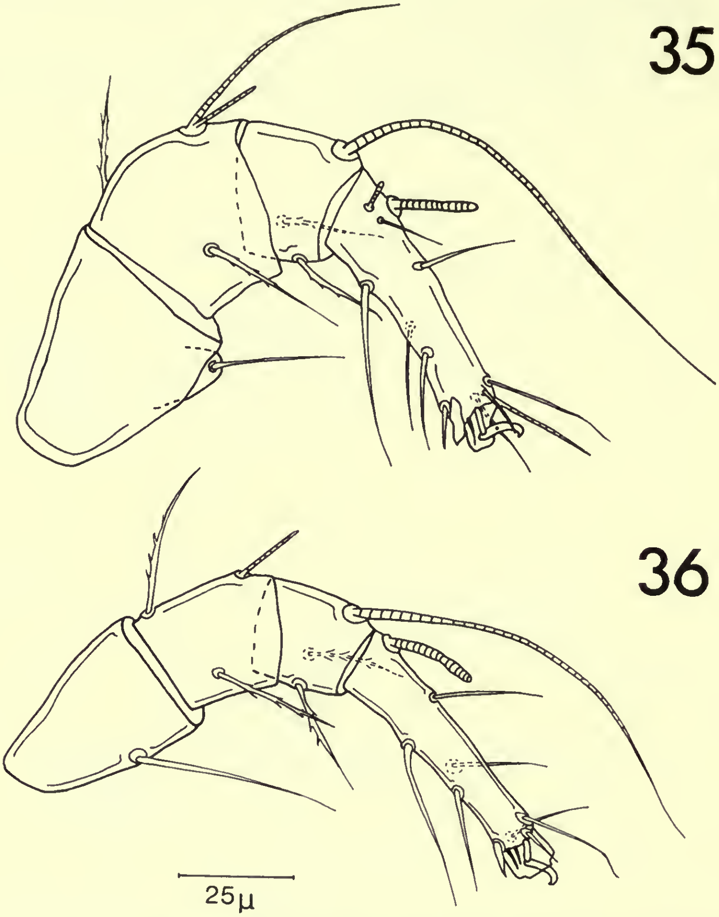


FIGS. 33, 34. *Acarus calcarabellus sp.n.* Leg I chaetotaxy. 33, ♂; note absence of genual processes and small femoral spur. 34, ♀.

Plate I, fig. 1 and 2 illustrates that ω_1 of *A. immobilis* can vary in thickness. It is also true that setal length is variable. Therefore, the Formosan specimens may represent an extension of the variability already observed in populations from Europe and the Near East. Until such time as further populations become available from the Far East, these specimens must remain *incertae sedis*.

(ii) ***Acarus*** population ex cocoanuts, Brazil, imported into U.S.A., 1935.

One ♂, one ♀ and a tritonymph were taken from cocoanuts imported into San Francisco, from Brazil on July 7th, 1935. Coll. F. J. Phelan. U.S. National Museum collection, San Francisco number 5368.

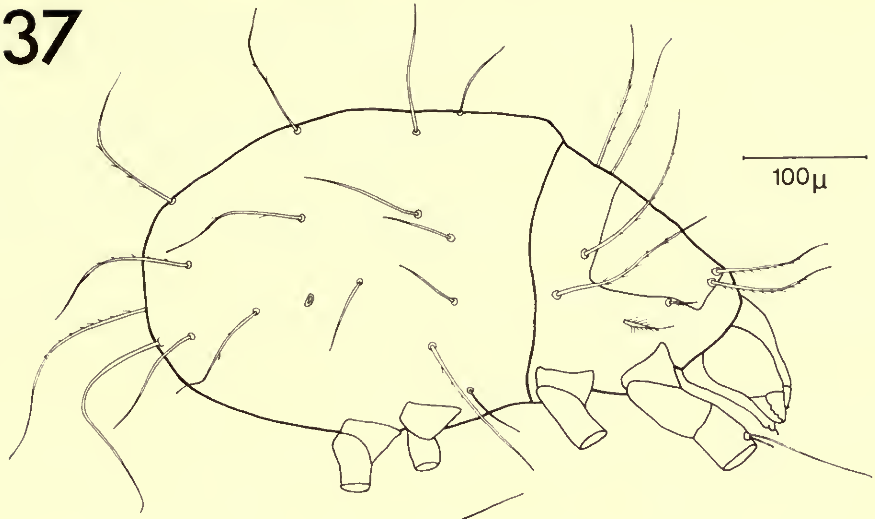


FIGS. 35, 36. *Acarus calcarabellus* ♂ holotype. Leg chaetotaxy (excluding trochanter segment). 35, leg I. 36, leg II.

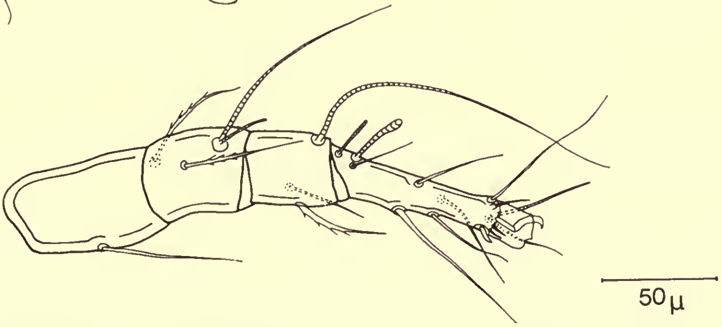
FEMALE (Text-fig. 39) : Dorsal hysterosomal setae relatively long, with d_2 and d_3 reaching or overlapping bases of next distal pair of setae. Scapular setae each bears five or more sets of pectinations but *all* setae of the hysterosoma are glabrous with fine endings. The supra-coxal setae are long and slender, bearing only seven pectinations (Text-fig. 39). Solenidion ω_1 has a shape which closely resembles that found in *A. immobilis* (Pl. III, fig. 3).

MALE : Represented by one poor specimen. Genual processes and tibial spur

37



38



FIGS. 37, 38. *Acarus* specimen. *incertae sedis* ex Formosan *Citrus grandis* fruit. 37, ♀ lateral view. 38, leg I of same ♀.

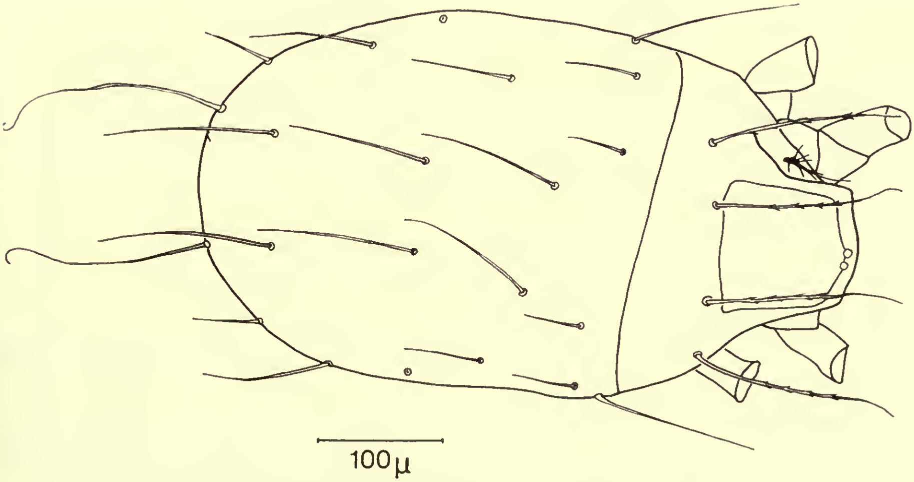


FIG. 39. *Acarus* specimen *incertae sedis* ex Brazilian cocoanut. ♀, dorsum.

normal. Idiosomal setae as for female except d_4 and *sc e* each bear two pectinations. Only one supra-coxal seta on specimen, this bears only four, long, slender pectinations. Solenidion ω_1 as for female.

Taxonomic position : This taxon combines the distinguishing characters of a number of the species described above. Solenidion ω_1 is similar in shape to ω_1 of *A. immobilis* (compare Pl. I, fig. 2 with Pl. III, fig. 3). However, the hysterosomal setae are too long and devoid of pectinations for it to be considered conspecific with *A. immobilis*.

The glabrous nature of the hysterosomal setae puts it close to *A. chaetoxysilos* and to the specimens *incertae sedis* ex China (see below). The long, slender, sparsely pectinated supra-coxal seta serves to distinguish it from both of these taxa. Since all the characters cited above are known to exhibit intra-specific variation, it is considered that the taxon be placed as specimens *incertae sedis* until further material becomes available.

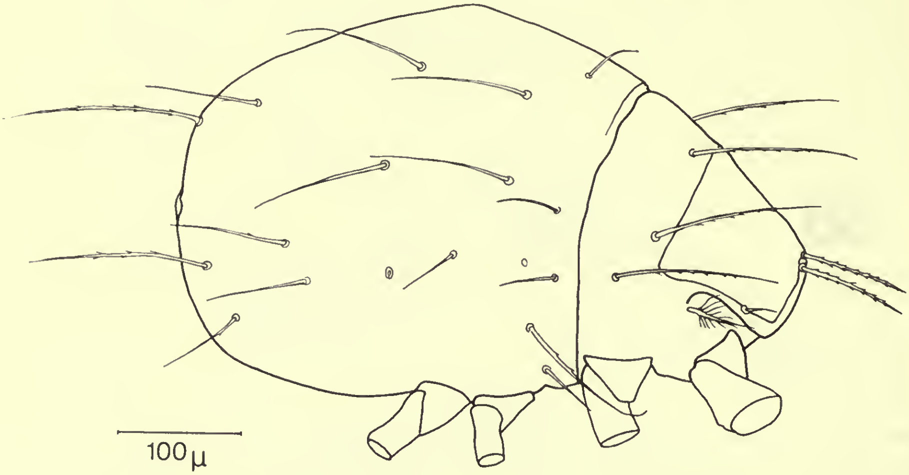


Fig. 40. *Acarus* specimen *incertae sedis* ex Chinese water-chestnuts. ♀, dorso-lateral view.

(iii) **Acarus** population ex Chinese water chestnuts, imported into U.S.A., Jan. 22nd, 1937.

The taxon is represented by one ♂ and ♀ on U.S. National Museum slide number 37-2183. One other female, not an *Acarus*, is also mounted on the slide. The material was imported from China into Chicago.

The specimens are close to *A. immobilis* but the dorsal setae are longer and less pectinate than those of *A. immobilis* populations examined to date (Compare Text-fig. 4a with 40).

7. RE-ATTRIBUTION OF MATERIAL LISTED AS SPECIMENS *INCERTAE SEDIS* IN GRIFFITHS 1964 (pages 453 to 457).

These were catalogued under the country from which they probably originated although some were collected at quarantine centres in the U.S.A. I shall re-list them as first published.

(i) BRAZIL (on orange navel end). Since I am now satisfied that in *A. immobilis* the dorsal idiosomal setae d_2, d_3 and d_4 may be longer than given in my original description, I place this specimen in *A. immobilis*.

(ii) NEW ZEALAND. Now considered to represent hybrids of the cross *A. siro* × *A. immobilis*.

(iii) FORMOSA. Remains as specimens *incertae sedis* (see p. 109).

(iv) JAPAN. Given specific rank in this paper (see p. 105).

(v) AZORES ♀ AND KENYA ♀. These were originally thought to represent intraspecific variation in *A. siro*. On the evidence illustrated in Text-figs. 2 and 3, I am now convinced that this is correct.

(vi) CHINA. Still placed as *incertae sedis* (see p. 112).

(vii) U.S.A., NEW MEXICO. Raised to specific level (see p. 102).

8. AN APPRAISAL OF THE *ACARUS* SPECIMENS CONTAINED IN THE OUDEMANS COLLECTION, RIJKSMUSEUM VAN NATUURLIJKE HISTORIE, LEIDEN.

I am most grateful to Dr. Van der Hammen of the Rijksmuseum van Natuurlijke Historie, Leiden, who kindly loaned the material in the Oudemans collection appertaining to the genus *Acarus*. Namely; slides labelled *Tyroglyphus farris*, *Tyroglyphus farinae* and *Tyroglyphus africana*. The mounting medium on many of the slides has deteriorated but the important morphological characters of most specimens can be resolved with phase-contrast equipment. This most interesting collection has been examined and specimens have been determined to species level according to the information obtained from my investigations into the genus *Acarus*.

(i) Material labelled *Tyroglyphus farris* Ouds.

It consists of seven slides representing material collected from three localities. The label on the left side of each of the slides has been crossed through by two pencil lines. Buitendijk (1945), in her catalogue to Oudemans' collection, states that the word 'fout' (error) is written on the drawings of *farris*, but the reason for this is unknown. I believe that Oudemans crossed through the slide labels and wrote 'fout' on his drawings when he decided, in 1925, that *farris* was a race of *farinae* and not a discrete species.

The left label of each slide bears the word '*type*' (in ink) in Oudemans' handwriting. Since his original description of *farris* is based on material which he collected at Arnhem in 1902, I have previously selected as lectotype the single male specimen mounted on the slide numbered 45 (Griffiths, 1962). Details of the slides are as follows: Catalogue numbers 43 and 44 :- Utrecht Sept., 1885. One chelicera and part of a gnathosoma is mounted on slide 43, which is in poor condition. Slide 44 consists of seven females, all of which are identifiable as *Acarus farris*. The habitat is not recorded. Catalogue numbers 45, 46 and 47 :- Arnhem February 1902; taken from cheese. The cover-slip of slide 45 is crazed but the diagnostic characters of tarsus II of the single male are plainly visible under a phase-contrast microscope (mag. × 800). Slides numbered 46, 47 and 48 are not in very good condition. They bear, respectively, single specimens of the tritonymph, protonymph and larva.

Catalogue number 49 :- Arnhem March 1909, *Mus decumanus*. The cover-slip is crazed and the seven tritonymphs mounted on the slide have shrivelled.

(ii) Material labelled *Tyroglyphus farinae* L. 1758.

It consists of twenty-seven slides (catalogue numbers 1 to 27), representing twenty-one collections made between 1898 and 1932 by various people. Details of these slides are listed below in the following manner :

Slide number :

L = Inscription on left label ; since the words '*Tyroglyphus farinae* L. 1758' appears on each label, they have not been repeated each time in the following notes.

R = Inscription on right label ; generally a record of date of collection, habitat, location and collectors' name.

This information is followed by my determination of the specimens on the slide, where this is possible, and remarks when necessary.

1. L. Female ds. ve.
R. Zuid Willems-varrt Brabant 9.viii.1918. Dr. G. Romyn prep. no. 196.
Two females both of which are *A. siro*.

2. L. Nph II. hypop. Kortharig ras.
R. Nest van *Talpa europaea* L. Sittard 12. 1911 F. Heselhaus. Eleven motile hypopi of *A. nidicolous sp.n.* Oudemans' comment 'Kortharig ras' [short-haired race] refers to the short scapular and dorsal setae peculiar to this hypopus.

3. L. Nph II hypopialis vent.
R. *Cucumis melo* en sativa. Zwyndrecht 20.5.1922.
Institut v. Plantensiekten Wageningen.

The morphology of dorsal and ventral surface of this single motile hypopus is extremely similar to that of an F_1 hybrid motile hypopus resulting from the cross *farris* × *immobilis*.

4. R. op Kass, Rykszuivel station Leiden; Dr. van Sillers Edt.
Eight specimens, comprised of a mixed population of *siro* and *farris*.
Taken from cheese, State Dairy Produce Station, Leiden, Holland.

5 and 6.
R. Hyacinthebol, Sassenheim Febr. 1924.
F. Schoevers Wageningen don.
Slide 5 is of nine males and slide 6 bears twenty-four females. This material represents a mixed population of *farris* and *immobilis*. Twelve of the specimens are *immobilis*, six are *farris*, nine appear to be hybrids and six I cannot identify because it is impossible to obtain a lateral view of solenidion omega$_1$.

7. R. Insection collectie Amsterdam, 1916. MacGillavry.

Sixteen hypopi (possibly taken from an insect specimen by MacGillavry). This slide is in a very poor condition. I can identify eight specimens as *farris* but the remainder cannot be identified.

8. L. Nph I dors. vent. lat.
R. in grutterswaren, Keuringsdienst Amsterdam. Oct., 1923.

Three protonymphs which judged on the size of spine S, are *siro*. Translation of details on right label is : 'in corn-chandlers wares, Inspection Service, Amsterdam'.

9. L. Male dors. vent. normal gebouwd ras.
R. Arnhem 27 Mei, 1898 Oudemans.

A very poor slide bearing two males which I believe are *A. siro*, but the specimens are too obscured to be absolutely certain. These specimens represent Oudemans' 'normal born race' in his discussion of races (Oudemans Feb., 1924).

10. L. Protonympha dors. vent.
R. op veegsel meelmager Arnhem 2.2.1902 Oudemans.

Five protonymphs, all *siro*; collected by Oudemans from old flour sweepings.

11. L. Nyph II hypop. dors. mooi exemplar 258.
R. *Mus rattus* L. Arnhem 8.10.1904. Oudemans.

This is a hypopus of *A. farris*.

12. L. male, zeer sterk ontwikkeld ras.
R. *Cavia cobdya*, Arnhem Feb. 1909 Oudemans.

One male *A. farris*. Translation of note on left label reads :- 'very strongly developed race'. Oudemans (Feb., 1924) gave this male as an example of a strong race having dark coloured legs. But, differing from other strong races in that tarsi of legs II, III and IV were long and slender; as long as the genu and tibia together. It is interesting to note that Oudemans did not recognise this specimen as *farris*.

13. L. nph. female, male.
R. in een gat in een appal. Arnhem 17-III-1918 Oudemans.

Three specimens too poor to be identified, together with one male which is *farris*. They were taken from a hole in an apple.

14. L. groot ras.
R. auf Kase, Bremen 16.9.1904 F. Koenike coll.

One male, one female, both *farris*. Oudemans (Feb., 1924) gave these as an example of a strong race which had shorter tarsi than the male on slide 12.

15 and 16.
L. 15- hypopi uit Nph I gekweekt
16- Nph II uit hypopi gekweekt.
R. Berlyn 14.5.1923, Hanna Schulze.

Slide 15 bears 8 motile hypopi of *A. farris* which emerged from protonymphs and slide 16 is of 3 tritonymphs which emerged from hypopi.

But, since I am unable to distinguish between nymphs of *farris* and *immobilis*, I cannot be certain to which species the tritonymphs belong.

17, 18 and 19.

R. Shag-tabak, Hamburg, Feb., 1928. Dr. L. Reh, visit.

Three slides, totalling fifteen females and one male; all are *A. siro*.

20. R. op vorkens-dormen Berlyn Aug. 1927. Dr. F. Zacher.

Twelve specimens all identifiable as *A. Siro*.

21 and 22.

L. Lv, Nph I, III, adulti.

R. *Evotomys glareolus*. Schreber Hemmelsdorper See. 10.4.1926 Erna Mohr.

There are over one hundred and fifty specimens on slide 21, which is not very clear. All the specimens which can be identified are *A. siro*. The single hypopus on slide 22 is definitely an *Acarus siro*. It is the only one in the whole collection. Presumably, these specimens were taken from the nest of a bank vole.

23. L. Printed label ACAROTHECA I-9 *Aleurobius farinae* (D.G.)

R. Printed label ITALICA. In farina, caseo, etc., Italia septentre. A. Berlese.

One male and one female. The male is an *Acarus farris* and the female is an *Acarus siro*.

Berlese used to make slides which he then sold to institutions and private collectors. Slide 23 is undoubtedly an example of this work. To each slide of any one species Berlese attached printed labels. The right-hand label of each was inscribed with identical information concerning the habitat of the species. Usually, this information was of a general nature, giving the habitat in which Berlese believed the mite was most commonly found. In this case he gave 'in farina, caseo, etc.,'. Since it is possible the mites may have been collected from some other habitat, this data is not necessarily true for these particular specimens.

24 and 25.

L. Nympha.

R. Steelgrove *Citrus aurantium* Zind Europa. Arnhem, Oudemans II, 1932.

Both slides have been re-mounted. I failed to find any specimens on either slide!

26. L. Nph II hyp. dors. vent.

R. *Osmoderma eremita* Scop. Weenen Aug., 1924.
H. E. Wickmann, legit Vitzthum donavit.

One hypopus of *A. farris* which presumably was taken from *O. eremita* (a species of the flower-beetles).

27. R. in een buisje met *Hevea* parasieten; Medan, Deli Proepstation AVROS Mei, 1918.

Two males, one is *siro*, the other specimen is crushed and cannot be identified. Translation of words on right label reads—'in a tube with *Hevea* parasite, Medan, Deli Agricultural Research Station'.

(iii) Material labelled *Tyroglyphus africana*

This consists of one slide labelled as follows:

Catalogue no. 1,
L. *Tyroglyphus africana* (Oudms) female, dors *type*.
R. *Platygenia barbata* (Cetonide) Togo (W. Afr.)
H.Voigts 10.ix.1901.

A single female which is undoubtedly an *Acarus siro*, placed in synonymy in Griffiths 1964.

9. SUMMARY

Ten species taxa are recognised; four are described for the first time, two of which were previously considered as specimens *incertae sedis*. A key to adults is provided.

Generic characters together with interspecific and intraspecific variation are reconsidered. An appraisal is made of the *Acarus* specimens contained in the A. C. Oudemans collection, Rijksmuseum van Natuurlijke Historie, Leiden.

10. ACKNOWLEDGEMENTS

I am most grateful to the many acarologists who were sufficiently interested in my first revision of *Acarus* to send me material which they considered to be unusual, and which I have subsequently used as the basis of this new study. I am particularly indebted to Dr. E. W. Baker, United States National Museum, Washington, Dr. E. van Eyndhoven, Zoological Museum, Amsterdam, Dr. D. Furman, Division of Parasitology, University of California, Dr. D. Johnston, Institute of Acarology, Ohio State University, and Dr. W. Knulle, Acarology Laboratory, Department of Zoology and Entomology, Ohio Agricultural Research and Development Centre. I am most grateful to Dr. L. van der Hammen, Rijksmuseum van Natuurlijke Historie, Leiden, for the loan of Oudemans' material.

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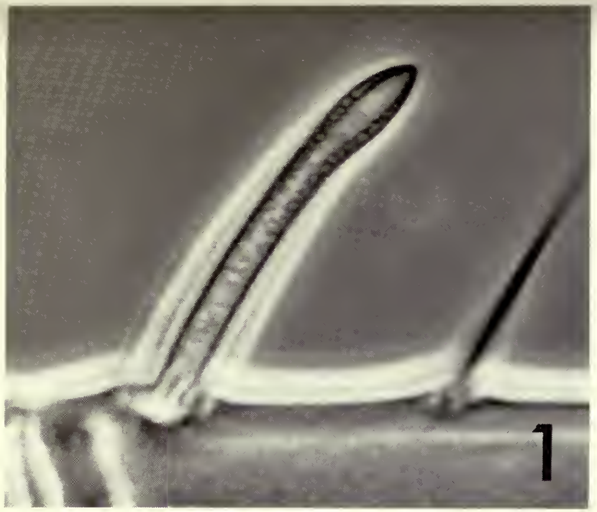
C

PLATE 1

Lateral view of solenidion omega$_1$ (ω_1) situated on tarsus II. ×2250

FIGS. 1 & 2. *Acarus immobilis* Griffiths.
FIG. 3. *Acarus gracilis* Hughes.
FIG. 4. *Acarus siro* L.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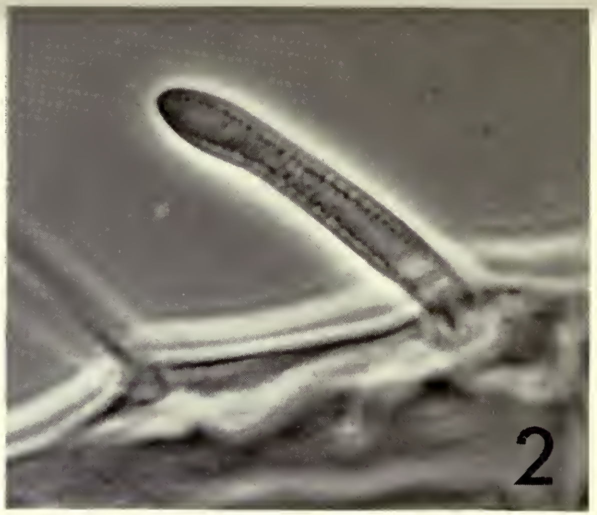
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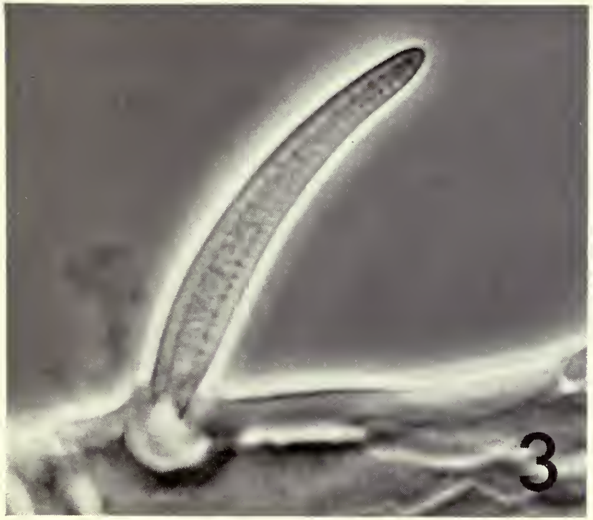
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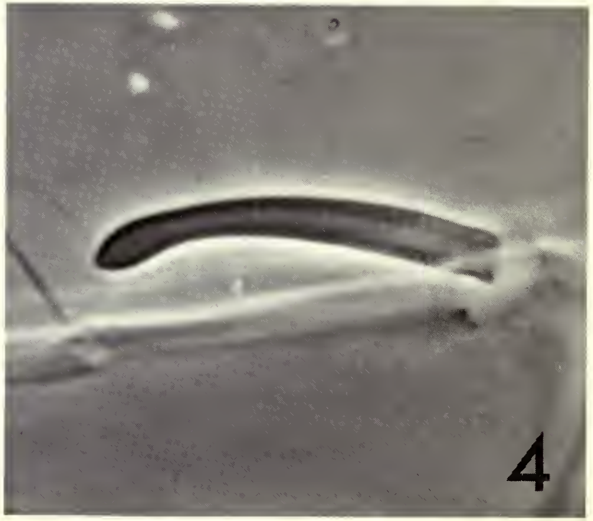
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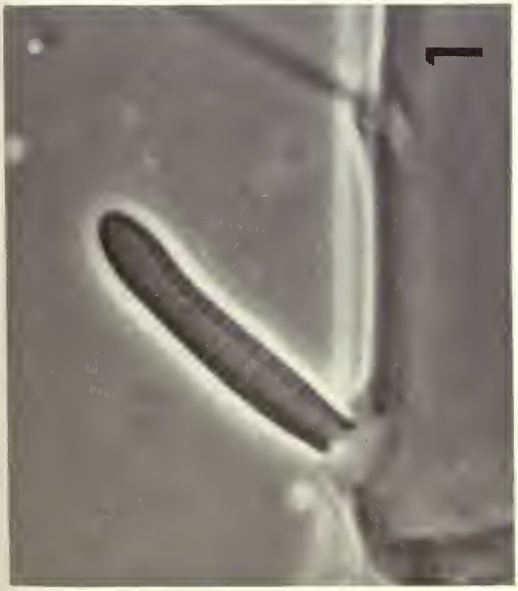
PLATE 2

Lateral view of solenidion omega$_1$ (ω_1) situated on tarsus II. ×2250

FIG. 1. *Acarus farris* (Oudemans)
FIG. 2. *Acarus calcarabellus sp.n.*
FIG. 3. *Acarus nidicolous sp.n.*
FIG. 4. *Acarus macrocoryne sp.n.*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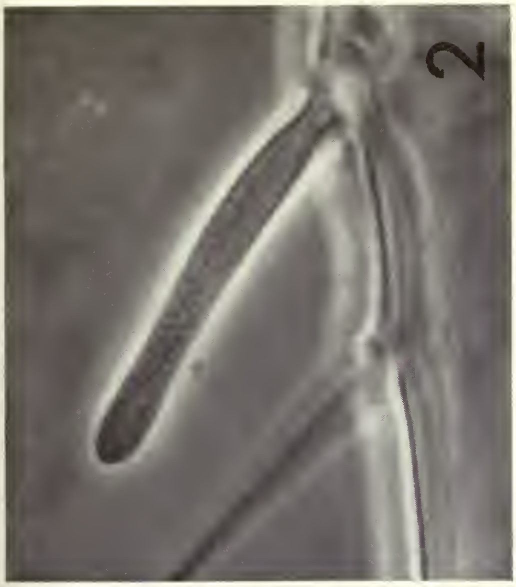
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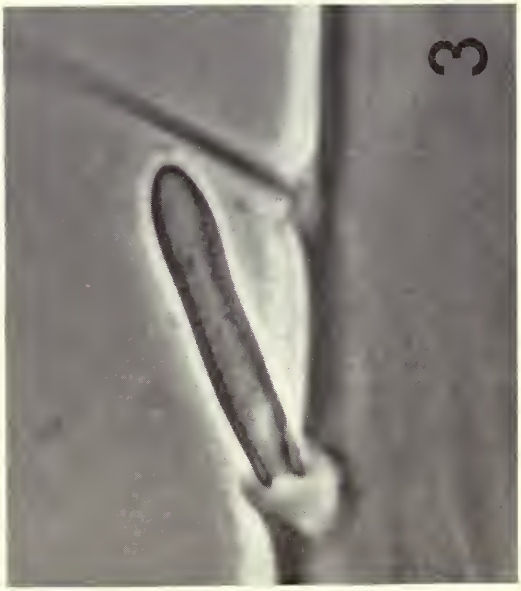
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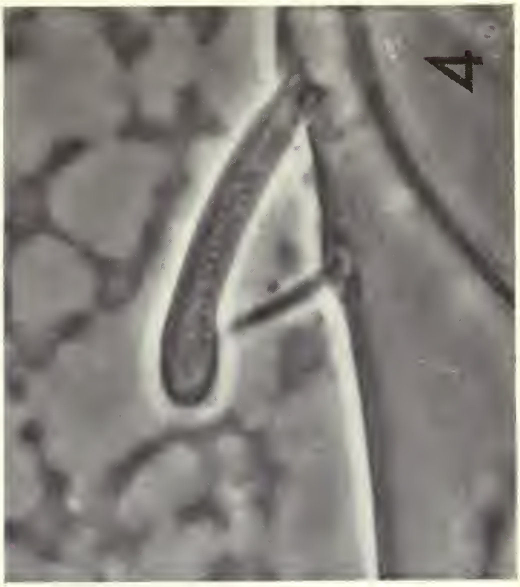
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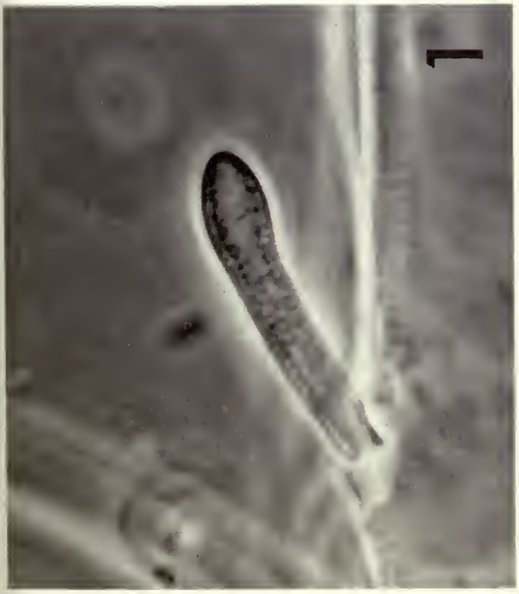
PLATE 3

Lateral view of solenidion omega$_1$ (ω_1) situated on tarsus II. × 2250

FIG. 1. *Acarus* specimen *incertae sedis* ex Chinese water-chestnuts.
FIG. 2. *Acarus chaetoxysilos sp.n.*
FIG. 3. *Acarus* specimen *incertae sedis* ex Brazilian cocoanuts.
FIG. 4. *Acarus* specimen *incertae sedis* ex Formosan *Citrus grandis* fruit.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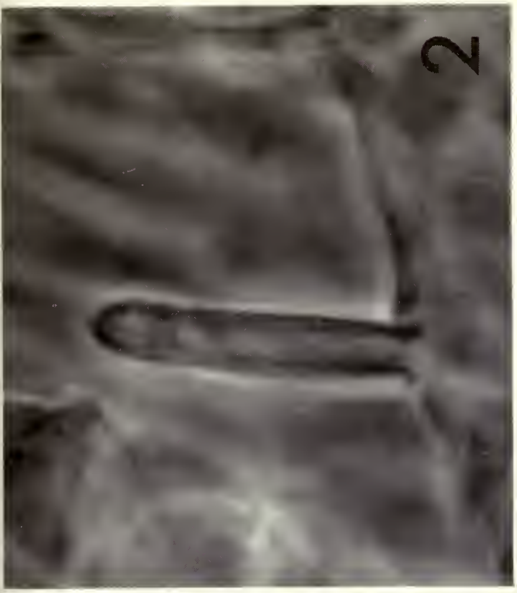
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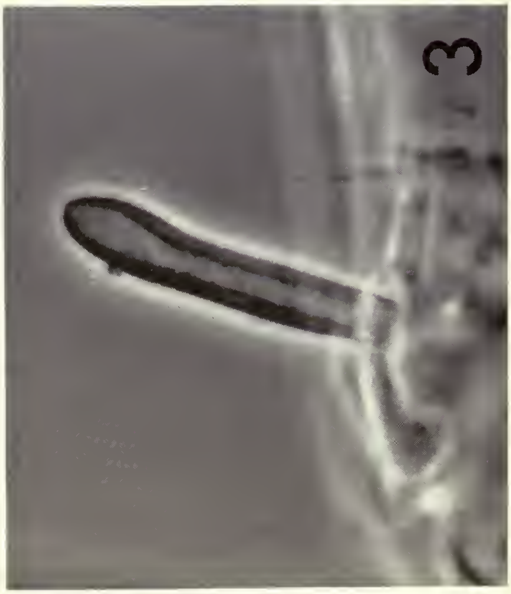
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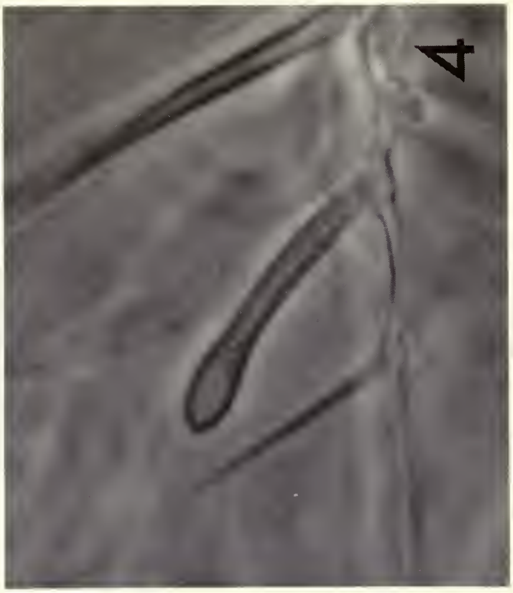
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PLATE 4

FIG. 1. *Acarus siro* L. ♀. Apex of tarsus I showing large spine *s* curving away from pulvilus.

FIG. 2. *Acarus immobilis* Griffiths. ♀. Apex of tarsus I showing small spine *s* curving towards pulvilus.

FIG. 3. *Acarus siro* L. A scanning electron micrograph of Grandjean's organ showing its structure and position. × 3200

FIG. 4. *Acarus siro* L. A scanning electron micrograph of the supra-coxal seta. × 3200

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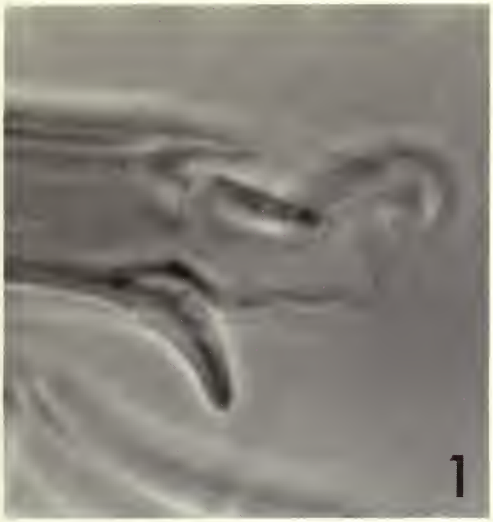
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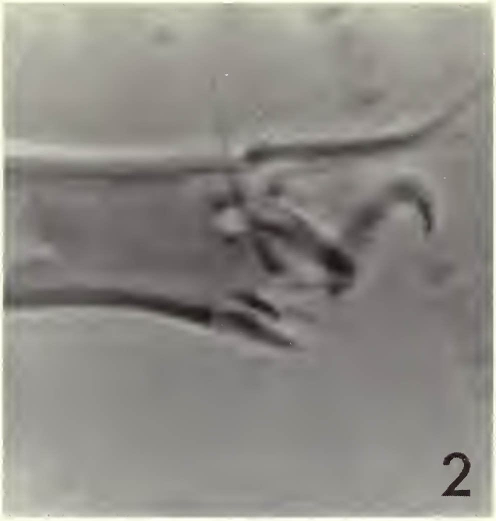
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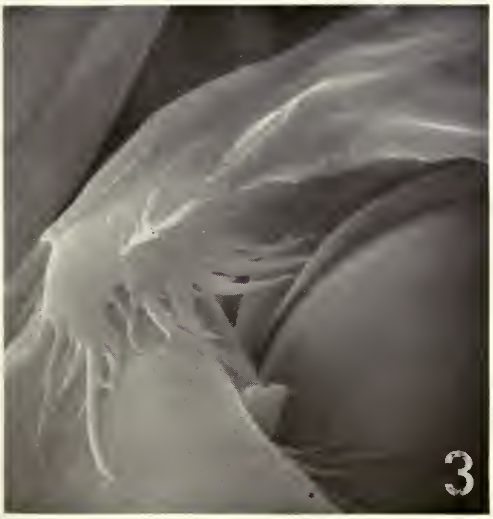
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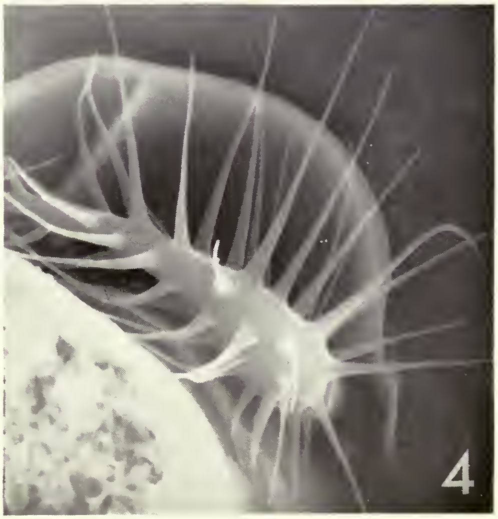
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SKULL AND SWIMBLADDER CONNECTIONS IN FISHES OF THE FAMILY MEGALOPIDAE

P. H. GREENWOOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 19 No. 3
LONDON : 1970

SKULL AND SWIMBLADDER CONNECTIONS IN FISHES OF THE FAMILY MEGALOPIDAE

BY

PETER HUMPHRY GREENWOOD

Pp. 119–135; 3 *plates,* 2 *text-figures*

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SKULL AND SWIMBLADDER CONNECTIONS IN FISHES OF THE FAMILY MEGALOPIDAE

By P. H. GREENWOOD

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INTRODUCTION

THE only detailed account of connections between the swimbladder and the otic region in megalopid fishes is that given by de Beaufort (1909), who described the Indo-Pacific Oxeye, *Megalops cyprinoides* (Brouss.). The closely related Atlantic species *Tarpon atlanticus* (C. and V.) is mentioned in de Beaufort's paper solely by the quotation of Hyrtl's (1855) brief description of the swimbladder. No comparative study, or comment, was made by de Beaufort.

Hyrtl's remarks are rather vague and would not lead one to suspect the existence of any marked interspecific differences in swimbladder anatomy. Later authors, as did de Beaufort, have tacitly assumed that the swimbladder and its otic connections are alike in both species.

Externally, the two species are very similar, and there is still a great deal of uncertainty about the generic status of the Atlantic Tarpon. Some authors treat it as a monotypic genus, *Tarpon atlanticus*, while others refer it to the genus *Megalops* (see Hollister, 1939, and Hildebrand, 1963, for further discussion). This problem will be considered anew in the light of the marked interspecific differences which I have found in many details of the skull-swimbladder linkage, and in the otic region of the skull.

Other taxonomic problems, but particularly the relationship between the Elopomorpha and the Clupeomorpha, will also be discussed (see Greenwood *et al.*, 1966).

THE LINKAGE BETWEEN SKULL AND SWIMBLADDER IN *MEGALOPS CYPRINOIDES*

In general, my investigation of the swimbladder in this species confirms the description given by de Beaufort (1909). The situation is redescribed here in some detail mainly to serve as a basis for comparison with *Tarpon atlanticus* (see pp. 125–8).

The soft tissues. There is one aspect where de Beaufort and I differ, and that is in our interpretation of the outer thickened tunic which covers the precoelomic extension of the swimbladder.

The tunic is identified by de Beaufort as swimbladder wall which has become greatly thickened and differentiated into an anterior, transversely aligned, " U "-shaped portion linking the periotic bullae with the longer egg-shaped part running forward from the pneumatic duct (see de Beaufort, 1909, p. 529; fig. 2, and plate 29, fig. 3). de Beaufort does not identify precisely which of the swimbladder tunics is thickened, but his figures and description would seem to imply that it is the tunica externa. Certainly his figure 2 shows the egg-shaped portion as continuous with the outer wall of the main bladder. He is quite explicit in identifying the tissue which enters the periotic bullae (the " U "-shaped part remaining outside) as tunica interna.

I find, however, that the thickened tissue of the egg-shaped portion is actually continuous with the much thinner peritoneal membrane covering the ventral and lateral aspects of the main swimbladder. Although the thick and thin parts of the peritoneum are continuous, there is no obvious gradient in thickness between them. Instead, there is a clear-cut line of demarcation running obliquely upwards and posteriorly from a point just anterior to the pneumatic duct. Without special care in dissection, the peritoneum parts cleanly along this line. The thin tissue then collapses and adheres closely to the swimbladder, while the thick walled egg-shaped portion retains its shape. In this condition the egg-shaped part certainly does not appear to be part of the peritoneal lining, but nor does it seem to be part of the swimbladder, which can be seen lying within it.

From a careful dissection of the tissues involved, and considering that the egg-shaped portion is continuous with the peritoneum, I find it difficult to interpret the precoelomic, thick-walled tunic as being derived from intrinsic swimbladder tissue. Instead, I would interpret it as being derived from the peritoneum; in effect, an evagination of the transverse septum. Thus, the precoelomic portion of the swimbladder, like the coelomic part, lies in a peritoneal cover.

As far as can be determined from gross dissection and microscopic studies of sections through a juvenile fish (*ca.* 5 cms standard length), the tunica externa (*sensu* Fahlén 1967) of the swimbladder is present throughout its precoelomic extension, apparently including the vesicles which lie within the periotic bullae. Further histological study on better preserved material is, however, necessary to confirm these points.

The beginning of the precoelomic peritoneal conduit for the swimbladder is taken to be the line of demarcation between thick and thin tissue (see above); dorsally, the thick tissue is closely associated with the 6th and 7th vertebrae. As de Beaufort noted, the main part of the conduit is approximately ovoid in form. Anteriorly (below the 1st or second vertebra) it bifurcates to form the " U "-shaped arms associated with the base of the skull, and extending upwards to the openings of the periotic bullae. At the point of bifurcation, the lumen of the ovoid body is deeply constricted, but it immediately expands in the base of the " U "-shaped arms.

Superficially, the egg-shaped body has, in preserved material, a silvery-white colour. Under moderate magnification the tissue appears to be made up principally of horizontally aligned, elongate, parallel and slightly sinuous fibres. Dorsally, this part of the conduit is firmly attached to the ventral and ventrolateral face of the vertebral column. The tissue is thickest along this line of attachment, and it surrounds the basal portion of several ribs which, in consequence, seem to emerge through the wall of the conduit. The point at which the egg-shaped body bifurcates to form the " U "-shaped part is clearly defined externally as well as internally. The " U "-shaped part has very thick walls, and in preserved specimens is yellowish-white in colour. Each arm of the " U " is only half a hollow cylinder but the transversely aligned basal part is a complete cylinder. The arms lie somewhat obliquely forward; the edges of each hemicylinder are closely applied to the skull. Anteriorly and dorso-anteriorly each arm is attached to the intercalar of its side, anteroventrally to the basioccipital, and posteriorly to the exoccipital. The cylindrical transverse part of the " U " is firmly attached to the base of the centrum fused with the basioccipital.

The precoelomic extension of the swimbladder is variously modified. Posteriorly, it differs but little from the region immediately behind the pneumatic duct, and like that region has a non-alveolate inner surface. (For a description of the alveolate main bladder, see de Beaufort, *op. cit.*). Further forward, the cross-section narrows rather rapidly until, at a point about half-way between the anterior bifurcation and the pneumatic duct, the bore is reduced to a narrow duct. As the bore narrows the wall thickens so that over its anterior third the swimbladder has a characteristic appearance, rather like a short section of plastic tubing. Throughout its passage in the peritoneal conduit, the swimbladder is loosely attached to the conduit walls by thin strands of connective tissue.

The thick-walled tube fills the narrow lumen which connects the " U "- and egg-shaped portions of the conduit. It penetrates for a short distance into the base of the " U ", and then bifurcates into two, thin-walled tubes, each of which completely fills the space between the skull and peritoneal wall in its arm of the " U ". On entering the periotic cavity each tube again expands to form an even thinner-walled vesicle, the periotic vesicle. The outer wall of the periotic vesicle is closely applied to the inner walls of its bony periotic bulla, with diverticula extending into the various recesses of the bulla's inner wall (see below).

Unfortunately, my material is not suitably preserved for detailed histological examination. Thus I cannot determine definitely if both swimbladder tunics contribute to the thick-walled tubular part; nor is it certain whether the periotic vesicle is formed from both tunica interna and externa or from the interna alone.

de Beaufort believed that only the tunica interna lined the periotic region, but then he apparently thought the tunica externa formed the "U"-shaped part of the conduit and therefore remained outside the bulla.

Otic region of the skull. Although the periotic swimbladder vesicles are completely surrounded by bone, they are nevertheless strictly extracranial in position, and lie alongside the lateral skull wall.

Each vesicle lies partly in a horizontally aligned, almond-shaped depression formed in the outer wall of the otic region (*i.e.* in the prootic, basioccipital and exoccipital bones). The greater volume of the chamber is, however, provided by the concave inner face of a shield-like extension from the intercalar. The shield reaches outwards and lateral to the depression in the otic wall, and forms the lateral and ventral walls of the periotic bulla. In other words, this hypertrophied portion of the intercalar forms a false lateral wall to the otic region (see Plate, 1, Fig. 1). The space between it and the true lateral skull wall (formed by prootic, basi- and exoccipital bones) being occupied by the swimbladder vesicle. Ridewood's statement (1904, p. 62) that " *Megalops* has a cavity *in* its opisthotic . . . " (italics mine) is inaccurate.

There are three, inwardly directed diverticula from the medial (*i.e.* skull) wall of each chamber. From the anterior part there is, ventrally, a broad, deep pit into the floor of the prootic bridge over the myodome. The opening into this diverticulum lies immediately below the anterior tip of the saccular recess in the prootic; the diverticulum of each side is separated in the midline by a thin bony wall. From the posterior part of the chamber there is a dorsomedially directed pit in the exoccipital, and a ventromedially orientated one into the basioccipital. In a dry skull, the ventromedial pits from each side meet one another in the midline of the basioccipital, and are continuous, forming a narrow transverse tunnel underlying the posterior part of the saccular recess. In an alizarin preparation, however, there is a thin bony partition between the medial tips of the diverticula. A foramen (situated immediately below the opening for the hyomandibular branch of the facial nerve) opens into the anterior part of the periotic bulla.

de Beaufort's description of the periotic chamber implies that it is divided into anterior and posterior parts, but none of the specimens that I have examined clearly shows any such division.

The bones forming the inner wall of the chamber (*i.e.* the skull wall) are thick and without foramina or fenestrae. Consequently the periotic swimbladder vesicles are nowhere in direct contact with the sacculus or utriculus (*cf.* the condition in Clupeomorpha where there is a direct contact with the utriculus; see Wohlfahrt, 1936).

The myodome in *M. cyprinoides* extends below almost the entire length of the saccular cavity, and the periotic bulla is entirely above and lateral to the myodome.

The intercalar (opisthotic of Ridewood, *op. cit.*) is a large bone of complex shape. For descriptive purposes three parts can be recognized; a relatively small dorsoposteriorly situated basal portion, an expanded lateral shield-like part, and an anterodorsally placed saddle-like wing (see Plate 1, Figs. 2A & B).

The basal part is roughly ovoid in shape, and of rather spongey texture; it has firm sutural unions with the exoccipital medially and the pterotic dorsally.

From the ventrolateral aspect of the basal part there is a short, broad, pedicel connecting it with the expansive, medially concave lateral shield. Posteriorly, the shield is suturally joined with the exoccipital (where it forms the floor to the foramen for the head vein and glossopharyngeal nerve); ventrally there is a suture with the basioccipital, and anteriorly one with the prootic.

The relatively deep dorsoposterior margin of the lateral shield curves medially and somewhat ventrally before expanding to form the broad, saddle-shaped wing. This portion provides the posterior part of the dorsal roof to the periotic bulla. Medially, the hind part of this roofing wing extends upwards and surrounds the basal portion (to which it is very closely applied); it also forms a backwardly directed, almost completely closed groove lying lateral to the basal ovoid (a narrow diverticulum from the periotic vesicle occupies at least part of this groove). The main body of the saddle expands ventrolaterally, and overlaps the upper margin of the lateral shield. In lateral view, the saddle-like wing appears to be an independent crescentic bone closely applied to both the basal part of the intercalar and to its lateral shield-like expansion; the impression is enhanced by the fact that, posteriorly, the crescentic element is suturally joined to a dorsal projection from the shield. However, when the intercalar is isolated from the surrounding skull bones its integrity is at once apparent.

Ridewood (*op. cit.*, fig. 12B, and p. 44) misinterprets certain relationships between the intercalar and its neighbouring bones. He describes the posterosuperior part as " . . . small and wedged in between the main part of the exoccipital and the part of the bone that forms the posterior border of the subtemporal fossa". The bone which he identifies as part of the exoccipital is, in fact, the posterior, upwardly directed groove formed by the saddle-like wing of the intercalar (*cf.* Plate 2, with Ridewood's fig. 12B).

There are no obvious ontogenetic changes in the morphology of the skull wall in the otic region, such as are seen in *Tarpon atlanticus* (see page 128).

SKULL AND SWIMBLADDER LINKAGE IN *TARPON ATLANTICUS*

In its basic features, the swimbladder-skull connection in this species resembles that of *Megalops cyprinoides*. The chief differences lie in the absence of any contribution from the intercalar to the wall of the periotic chamber (which is formed entirely from the peritoneal tissue), a simpler form of precoelomic peritoneal conduit, and the absence of a thick-walled section in the precoelomic swimbladder extension.

The soft tissues. The precoelomic prolongation of the swimbladder originates immediately anterior to the pneumatic duct. It is of slightly narrower diameter than the main bladder at that point, and is composed of very thin tissue. It almost fills the peritoneal conduit (see below), but, except for a short distance posteriorly in the midline, is free from the conduit walls. The lumen of the swimbladder decreases but slightly as it runs forward. At a point below the first vertebra the bladder divides into two, each arm then passing forward within the periotic chamber. These periotic vesicles are, like those of *Megalops*, very thin-walled; unlike that species there is, in *Tarpon*, no thick-walled tube immediately preceding the point of bifurcation.

The main (*ie.* coelomic) part of the swimbladder, like that of *Megalops cyprinoides*, is alveolate; the description given by de Beaufort (*op. cit.*) for that species could well apply to *Tarpon atlanticus*.

The peritoneal conduit surrounding the precoelomic swimbladder extends from about the 13th vertebra to the 1st vertebra. It is closely applied to the ventrolateral face of the vertebral column and is perforated by the 12th and 13th ribs posteriorly and the first five or six ribs anteriorly. Throughout its length the conduit is of almost uniform diameter, and its walls are of uniform thickness. Unlike *Megalops*, there is no deep ventral groove between the main body of the conduit and the otic arms, which in *Tarpon atlanticus* are just hemicylindrical lateral extensions of the median tube.

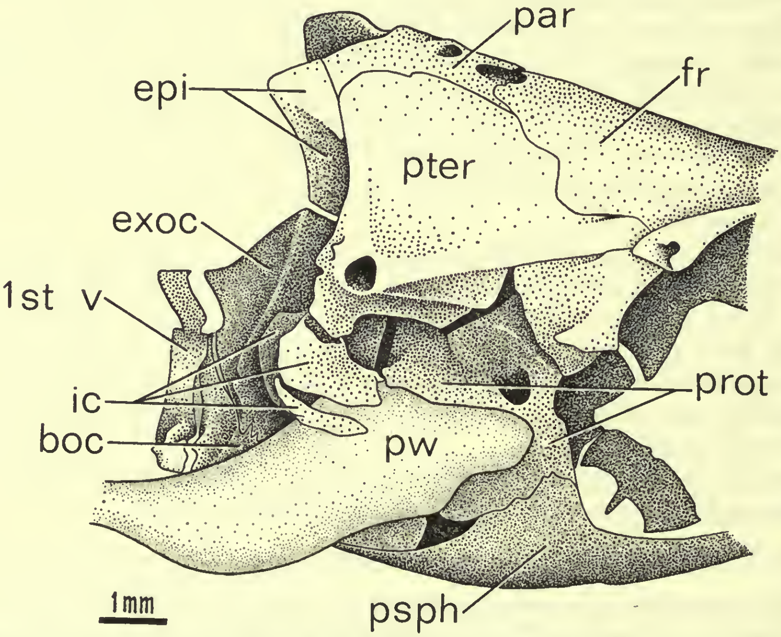

Fig. 1. *Tarpon atlanticus*. Otic region of skull (right) in a specimen 91·0 mm S.L. to show the periotic vesicle (p.w.) *Drawn by Sharon Lesure*

The otic arms arise at about the level of the first vertebra and run forwards and upwards at a slight angle (see text fig. 1). The ventral and median part of the main tube is, at the point of otic arm divergence, closely applied to the basioccipital.

Each hemicylindrical otic arm extends forward almost to the anterior margin of the prootic. Dorsally it is attached to the lower margin of the exoccipital, to the lower limb of the intercalar (see page 127), along the ventral part of the upper intercalar limb, and along the prootic (following a line level with the intercalar-prootic bridge). Ventrally it is attached to the ascending limb of the parasphenoid (its posterior margin), and to the basioccipital along the parasphenoid-basioccipital suture; the margin of the tube skirts the base of the first infrapharyngobranchial where the latter articulates with the ascending parasphenoid limb.

Otic region of the skull. From the description given above it will be seen that *Tarpon atlanticus*, unlike *Megalops cyprinoides*, has the entire wall of the periotic cavity formed from peritoneal tissue. The intercalar in *Tarpon* serves only as a point of attachment and, to a certain extent, suspension for the peritoneal tissue. In *Megalops* it will be recalled, the peritoneal wall is replaced by a bony plate developed from the lower limb of the intercalar.

The medial wall of the periotic chamber (which is, of course, the lateral skull wall) is formed chiefly by the basioccipital and prootic with a small contribution posteriorly from the exoccipital (Plate 3, Fig. 1). The line of contact between the prootic and basioccipital runs obliquely upwards and backwards; near its antero-dorsal tip, the basioccipital margin diverges slightly from that of the prootic, and a small triangular fenestra is formed. It opens directly into the saccular recess. The fenestra is most obvious in small specimens but it is still present in the largest skull examined (21 cms long). In all specimens throughout the size range available (skull lengths 4·3–21·0 cms) certain areas of the bony inner wall to the periotic cavity are thinner and more flexible than are other areas. The flexible zone is usually centred in the basioccipital, but may include the posterior part of the prootic as well. This condition contrasts markedly with that in *Megalops* where there is neither a fenestra nor thinning of the otic bones. In fact, the otic bones in *Megalops* are noticeably thicker and denser than those of *Tarpon*.

Pronounced ontogenetic changes take place in the morphology of the otic region, particularly with regard to the relative position of the saccular cavity. These changes are discussed below.

The intercalar is a large bone of somewhat complex form (Plate 3, Fig. 2A & B), but relatively simpler than that of *Megalops* (see page 124). Again, three regions can be recognized. The ovoid basal portion fits deeply into the exoccipital; the pit in which it is accommodated lies immediately above the foramen for the vagus nerve. Both the intercalar base and the walls of the pit are deeply ridged, the ridges from the two bones interdigitating.

Two limbs arise from the basal portion. One (the broader and more substantial) is crescentic in lateral outline. Its flattened horizontal portion extends forward to meet the prootic; the vertical portion curves dorsally and articulates with the pterotic. Medially the stout pedicel connecting this limb with the base is firmly articulated with the exoccipital.

The other limb lies below the crescentic one, is less substantial and, apart from its curved posterior margin (which serves as a pedicel) is almost horizontally aligned; it is slightly longer than the crescentic limb (see Plate 3, Fig. 1).

In fishes with a skull length of < 20 mm, the lower arm is well-separated laterally from the upper crescent, but in larger individuals (skull lengths 55 mm and above) the two arms are in contact for most of their lengths (*cf.* text fig. 1, and Plate 3, Fig. 1).

Four levator muscles from the 2nd–4th gill arches originate on the ventral and posterolateral aspects of the lower intercalar limb; the suprapharyngobranchial of the first gill arch articulates near the anterior tip.

Comparing the intercalar of *Tarpon* with that of *Megalops* it is clear that the expanded, shield-like part in *Megalops* corresponds to the lower limb in *Tarpon*, and that the dorsal, crescentic limb in that species is the homologue of the saddle-shaped wing in *Megalops*. Because the upper crescent in *Tarpon* has a more definite pedicel from the basal part, the base itself has no contact with the pterotic (that contact being effected through the pedicel).

Ontogenetic changes in the shape of the lateral skull wall of the otic region were mentioned earlier. The bones involved are the basioccipital and prootic, especially the former. In all specimens less than 23 cms standard length (skull length 4·3 cms) the wall of the otic region (which is the inner wall of the periotic chamber) is slightly convex, bulging a little into the periotic chamber. The large saccular otolith is visible through the thin bone; its ventral margin lies slightly above the level of the basioccipital-parasphenoid suture.

In two larger skulls (one 13 cms long from a fish 78·2 cms S.L., the other 21 cms long from a fish of unknown length) the lower part of the otic wall (particularly the basioccipital) is deeply concave (see Plate 3, Fig. 1). This once convex area now has the form of an almond-shaped depression. The depressed area lies principally in the basioccipital, below the ventral margin of the sacculus, which now lies in the same horizontal as the lowest point on the ventral intercalar arm. In the 13 cm skull there are two depressions (one in the basioccipital, the other in the prootic) separated by a narrow ridge (see Plate 3, Fig. 1). The posterior, almond-shaped depression in the basioccipital is the larger of the two. In the 21 cm skull, the depressions are confluent.

I have been able to examine only one skull of an intermediate size (5·5 cms, from a fish 31 cms S.L.). Here there is a noticeable concavity in the wall of the basioccipital, posterior and a little ventral to the saccular recess. There is also a shallow indentation of the prootic (just anterior to its suture with the basioccipital) below and in front of the saccular recess. Neither depression is as deep as those in the 13 cm skull, and the lower margin of the sacculus is still ventral in position.

Without more material from the upper part of the "intermediate" size range it is impossible to tell what growth changes are involved in producing the very characteristic form of the otic wall in " large " fishes. The dorsal migration of the saccular recess is particularly intriguing. Measurements made on the otic region in fishes of all available sizes do not indicate a marked differential growth anteroposteriorly or dorsoventrally in any part of the bones involved. There is, however, a suggestion that certain areas in these bones may grow inwards, thereby forming concavities laterally and, as the inner surfaces of the bones extend medially towards one another, the saccular recesses are forced upwards.

THE SACCULAR OTOLITH IN *MEGALOPS* AND *TARPON*

The sagitta in *Megalops cyprinoides* and *Tarpon atlanticus* differs in a number of features (see text fig. 2).

In *M. cyprinoides* the anterior outline is acute, with the ventral margin sloping gently upwards; in *T. atlanticus* it is relatively obtuse, with the ventral margin curved abruptly upwards near the tip. There is a distinct antirostrum and excisura in *M. cyprinoides* but neither is present in *T. atlanticus*. In that species, the dorsal outline posterior to the ostium is domed, whereas in *M. cyprinoides* the outline is but slightly curved.

The shape of the sulcus (which is somewhat constricted near its midpoint, has a broad and rounded cauda, and an expansive ostium) is alike in both species.

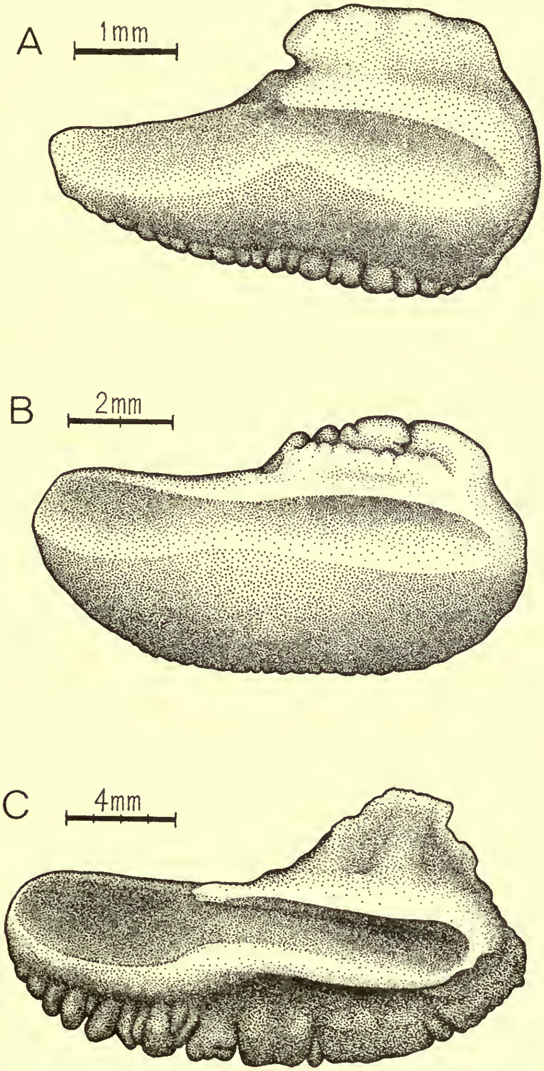

Fig. 2. Saccular otolith (sagitta) of A. *Megalops cyprinoides* (from a fish of unknown length, B. *Tarpon atlanticus* (from a fish 31 cms S.L.). C. *Tarpon atlanticus* (from a large specimen of unknown length). *Drawn by Sharon Lesure*

No details of possible growth changes could be determined from the *M. cyprinoides* sagittae available since both pairs are the same size (5·5 mm long). The two pairs of *T. atlanticus* sagittae show that in larger otoliths the dorsal outline is more produced, and the margin of the sulcus is raised and slightly thickened. The smaller sagitta

(10·0 mm long) is from a fish 31·0 cm S.L.; the larger otolith is 21·0 mm long but no record is available of the fish's size.

SWIMBLADDER-SKULL CONNECTIONS IN OTHER ELOPIFORM FISHES

An intimate and complex connection between the otic region and swimbladder exists only in the Megalopidae although in at least some Elopidae a simpler linkage is developed.

Elops lacerta C. and V. (two specimens, 190 and 270 mm S.L. examined) has two narrow, finger-like projections from the anterior part of the swimbladder. These extend forward from about the level of the first vertebra to a point just behind the saccular swelling on the basioccipital. Each projection is closely applied to the basioccipital and lies in a faint groove on that bone. A peritoneal sheath covers each diverticulum, but the tissue is not thicker or in any other way macroscopically distinguishable from the peritoneal layer covering the swimbladder itself.

de Beaufort (1909) describes paired anterior prolongations of the swimbladder in *Elops saurus* Linn., and notes that these reach only as far forward as the middle of the first vertebra. Cuvier and Valenciennes (1846, p. 373) also describe the paired diverticula but do not indicate how far forward they extend (except to note that there is no connection between the swimbladder and the interior of the skull). Finally it may be noted that Hyrtl (1855) makes no mention whatsoever of anterior swimbladder projections in this species.

In contradistinction to these earlier observations I find that the diverticula do extend forward onto the basioccipital (at least in a fish 280 mm S.L.), the situation being identical in all respects with that in *E. lacerta.* These discrepancies are difficult to reconcile; the size of the various fishes examined may, however, be partly responsible (see below).

In *Elops machnata* (Forsk.) (three specimens, two of 175 mm S.L., one 108 mm S.L.) there are two peritoneum covered anterior projections. These extend only to the level of the first vertebra in the larger specimens, and do not even reach that point in the smaller fish. Thus in this species it seems likely that the extent of diverticulum development is positively correlated with the size of the individual.

If in *E. saurus* there is a similar relationship, then the discrepancies between my observations and those of de Beaufort, Hyrtl, Cuvier and Valenciennes might be explained by their having dissected smaller fishes.

No linkage between skull and swimbladder is developed in the two species of Albuloidei I have examined.

In *Albula vulpes* (Linn.) de Beaufort (*op. cit.*) describes a pair of short blind-sacs from the anterior wall of the swimbladder at the level of the fourth vertebra. This is the condition I found in a specimen of 97 mm S.L. (BMNH 1862. 4. 24 : 31) ; the diverticula extend to the level of the anterior rim of the first vertebra. In contrast I could find no trace of diverticula in the other specimens (160 mm and 165 mm S.L. BMNH 1949. 11. 29 : 1 and 1855. 9. 19 : 875) I dissected ; in these fishes the forward end of the swimbladder is smoothly rounded and lies below the first vertebra. Likewise, I find no trace of the anterior diverticula in the swimbladder of *Pterothrissus gissu* Hilgen. (a single specimen 394 mm S.L., the type of *Bathythrissus* *dorsalis* Günther). Günther (1887), however, using the same specimen, described two short horns from the anterior wall of the swimbladder, which lies posteriorly in the visceral cavity and thus well behind the strongly developed transverse septum. The viscera of this fish are now in a rather poor state of preservation, and this could well account for my failure to find the horns.

Clearly the situation in elopoid and albuloid fishes requires further investigation on more species and over a wide size-range of individuals. Nevertheless, it does seem certain that no otophysic connection comparable in complexity with that of the Megalopidae, exists in the Elopidae and Albulidae.

DISCUSSION

The status of the genera MEGALOPS *and* TARPON. There is a great deal of uncertainty about the generic status of the Atlantic Tarpon (see Hildebrand, 1963) ; current opinion seems to favour it being congeneric with the Indo-Pacific species *Megalops cyprinoides.*

Jordan and Evermann (1896) erected the genus *Tarpon* for the Atlantic species, principally on the basis of it having a more posterior insertion of the dorsal fin than *Megalops cyprinoides.* Hollister (1939) showed, however, that the dorsal fin position is the same in both species, but that the ventral fins in *Tarpon* are nearer the snout. In addition she emphasized that *Tarpon* has fewer vertebrae (57, comprising 33 trunk and 24 caudal, compared with 68 [38 trunk and 30 caudal] in *Megalops*), and pointed out differences in the fin ray counts (12–15 dorsal, and 19–22 anal rays in *Tarpon, cf.* 19–21 dorsal and 24–27 anal rays in *Megalops*). Finally, Hollister drew attention to certain differences in the caudal fin skeleton, particularly the longer first uroneural in *Megalops* (see appendix, page 133).

A number of other osteological and soft anatomical differences associated with the swimbladder-skull connection can now be added to those already known. In particular may be noted the entirely peritoneal lateral wall of the periotic cavity in *Tarpon*, the more differentiated precoelomic extension of the swimbladder and its peritoneal sheath in *Megalops*, and the differences in the degree of development and complexity shown by the intercalar in the two species.

At the same time, one should not lose sight of the fact that basic similarity in the " bauplan " of the swimbladder-skull connection seems to stress the phyletic integrity of the two taxa. In this character it seems reasonable to consider the Atlantic species as the plesiomorph partner of the Indo-Pacific species. In other features it is impossible to obtain a clear-cut picture of relative plesiomorphy or apomorphy.

The nature of the interspecific morphological divergence in the swimbladder-skull connection would, nevertheless, seem to warrant the separation of the two species at generic level. Hence I propose to redefine the genera as follows :—

Genus *Megalops* Lacépède 1803 : megalopid fishes with an expanded arm of the intercalar forming the entire lateral wall of the large periotic bulla, which is thus completely bounded by bony walls ; precoelomic extension of the swimbladder with a short, thick-walled section, of narrow bore, immediately posterior to its division into two periotic vesicles ; peritoneal cover to the precoelomic swimbladder with a " U "-shaped otic portion leading to the periotic bullae anteriorly, and a longer, egg-shaped main body posteriorly ; 67 or 68 vertebrae; anterior tip of the first uroneural reaching the anterior part of the second preural centrum.

Genus *Tarpon* Jordan and Everman 1896 : megalopid fishes in which the intercalar does not contribute to the lateral wall of the periotic cavity, the latter bounded laterally by precoelomic peritoneal tissue only ; precoelomic peritoneal cover of the swimbladder extension passing smoothly into the otic arms forming the lateral walls of the periotic cavity ; precoelomic swimbladder extension without a thick-walled tubular portion ; 55–57 vertebrae; anterior tip of the first uroneural reaching the anterior part of the first preural centrum.

Relationships between the ELOPOMORPHA *and* CLUPEOMORPHA. Although Greenwood *et al.* (1966) included the superorders Elopomorpha and Clupeomorpha in a single division (later named the cohort Taeniopaedia, see Greenwood *et al.* 1967) they did so with little conviction, pointing out that if any relationship did exist it was a very distant one. Subsequent research has certainly not provided any new evidence to support any close phyletic grouping of the two taxa. In fact the new evidence indicates quite the contrary situation. For example, a detailed study of the clupeomorph family Denticipitidae (Greenwood, 1968) shows that its supposedly elopomorph-like characters (Greenwood *et al.*, 1966) are not of that nature, but are in fact, clupeomorph characteristics. The earlier confusion was due to insufficient knowledge of denticipitid anatomy. Other research on clupeomorph fishes (mostly unpublished, but see Patterson, 1970) has served to emphasize the uniqueness of this group in a number of specialized characters, characters which in all living and fossil elopomorphs show either no specialization at all or are developed along very different lines.

The swimbladder-otic linkage provides a good example of the latter condition. In the Clupeomorpha the swimbladder diverticula enter the skull, and the vesicles into which they expand are lodged within the bullae developed from the prootic and pterotic bones (or the prootic alone).

In megalopid Elopomorpha (the only members of the superorder with what could reasonably be considered a specialized otophysic connection) the linkage is entirely extracranial and involves different cranial bones. Such a condition could not be considered basic for the otophysic connection characterizing the Clupeomorpha. The otophysic connection found in the Elopidae (see p. 130), on the other hand, is of such a generalized type that it could be basic to either a megalopid or a clupeomorph type. As an indicator of phyletic relationship in this particular context it is valueless. Similar difficulties are encountered when one considers other characters ; indeed, the more one analyzes the Clupeomorpha and Elopomorpha, the more difficult it becomes to suggest a close relative for either taxon. In particular, any attempt to find a sister group (*sensu* Hennig, 1966) for the Elopomorpha is hampered by the extreme plesiomorphy of its basal, that is non-anguilliform, members.

Thus, since no positive evidence can be found to support the hypothesis that the Elopomorpha and the Clupeomorpha are each other's closest relatives, I propose that the Clupeomorpha be removed from the cohort Taeniopaedia.

This action, of course, raises the question of where the Clupeomorpha should now be classified. For the moment I can find no satisfactory answer. The clupeomorphs are not the sister group of the other primitive teleost cohort, the Archaeophylaces (osteoglossomorph fishes), and there is, at present, insufficient evidence to include them in the cohort Euteleostei (although this relationship is suggested by some characters). As a temporary expedient, then, the Clupeomorpha will have to be given cohort status and recognized as being a monophyletic group phylogenetically *incertae sedis*. Hopefully they will not remain too long in limbo.

SUMMARY

The skull-swimbladder linkage in *Megalops cyprinoides* and *Tarpon atlanticus* is described and compared. Although both species have the same fundamental bauplan, the linkage in *Megalops* shows greater differentiation of the tissues, in particular the peritoneal cover to the precoelomic swimbladder extension, and the involvement of the intercalar bone in forming a periotic bulla.

In *Tarpon* the peritoneal cover is a simple tube, and the intercalar does not contribute to the formation of a periotic bulla ; instead there is a periotic chamber with a non-bony lateral wall (formed from the peritoneal swimbladder sheath). Size correlated changes in the otic region are described for *T. atlanticus*; no such changes occur in *Megalops cyprinoides*.

Other members of the Elopiformes were also investigated, and a simple otophysic connection found in the three *Elops* species examined. *Albula* and *Pterothrissus* lack an otophysic connection.

The disputed generic status of the Atlantic Tarpon (*T. atlanticus*) is reviewed, and it is concluded that this species should be recognized as constituting a monotypic genus, albeit one closely related to *Megalops*. The two genera are redefined.

Finally, the phyletic relationships of the Elopomorpha is considered, particularly with regard to the supposed relationship of these fishes with the Clupeomorpha. There is apparently no positive evidence to support the idea of close affinity, and the Clupeomorpha are given cohort status.

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APPENDIX

NOTES ON THE CAUDAL FIN SKELETON IN *MEGALOPS* AND *TARPON*

I have examined the caudal fin skeleton in three specimens of *Tarpon atlanticus*, and four of *Megalops cyprinoides*. This structure is somewhat more variable in *M. cyprinoides* than was indicated by Hollister (1939). In contrast the characters of the caudal skeleton that are variable in *M. cyprinoides* are constant in *Tarpon atlanticus*.

Variability in *Megalops* involves the neural arches and spines associated with the first and second preural centra. Two of the four specimens have only a neural arch on the first preural centrum ; in the other two specimens this centrum carries a neural arch posteriorly, and an arch with short spine anteriorly. Three specimens (including the second pair noted above) have a neural arch with a fully-developed spine on the second preural centrum ; the fourth fish has an arch with very reduced spine, together with an arch and fully-developed spine articulating between this vertebra and the preceding one.

In all three *Tarpon* specimens there is a neural arch (but no spine) on the first preural centrum, and an arch with fully developed spine on the second preural centrum.

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LIST OF ABBREVIATIONS USED IN FIGURES

basph	basisphenoid
bic	basal part of intercalar
boc	basioccipital
boc dep	depression in basioccipital
epi	epiotic
exoc	exoccipital
fica	foramen for internal carotid artery
fn	foramen for unidentified branch of trigeminal nerve
fr	frontal
fu V	fused vertebral centrum
gr	groove
ic	intercalar
ica	saddle-like wing of intercalar
icagr	posterolateral wall of groove formed by saddle-like wing of intercalar
icb	lower limb of intercalar
icsh	shield-like expansion of lower intercalar limb
icu	upper limb of intercalar
io	orbitosphenoid
oaf	opening to foramen for orbital artery
ophv	opening for head vein
par	parietal
prot	prootic
prot dep	depression in prootic
psph	parasphenoid
pter	pterotic
ptf	posttemporal fossa
ptsph	pterosphenoid
pw	peritoneal wall to periotic chamber
soc	supraoccipital
sph	sphenotic
stf	subtemporal fossa
X	foramen for vagus nerve
1st v	first vertebra
1.	Foramen for head vein
2.	Foramen for hyomandibular branch of VII
3.	Foramen for orbital artery
4.	Foramen
5.	Foramen opening into periotic bulla

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PLATE 1

FIG. 1. *Megalops cyprinoides*. Otic region of skull in lateral view.

FIG. 2. *Megalops cyprinoides*. Intercalar, A, lateral aspect, viewed somewhat obliquely from above and anteriorly. B, dorsal aspect, the long axis of the bone aligned horizontally.

Drawn by Sharon Lesure

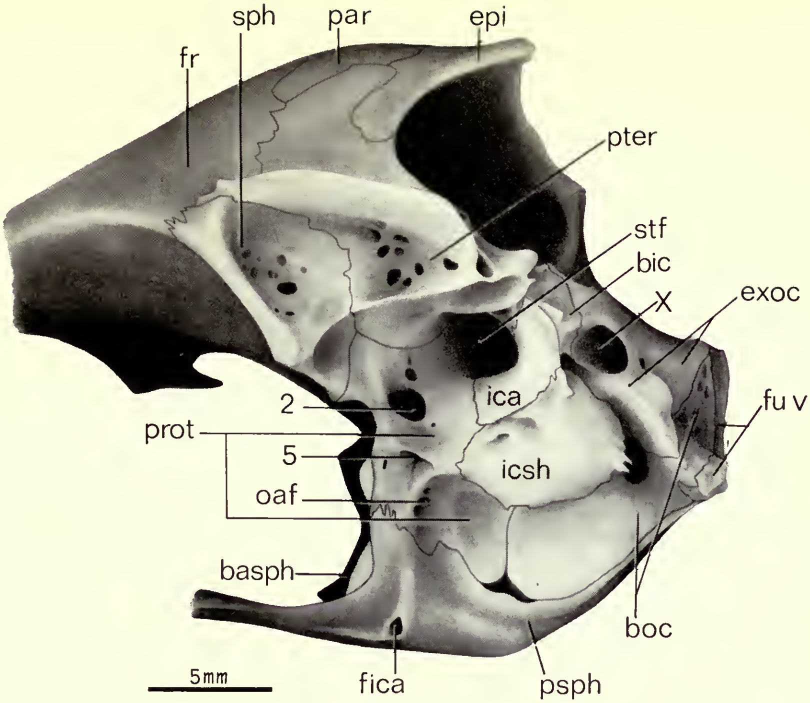
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Fig. 1

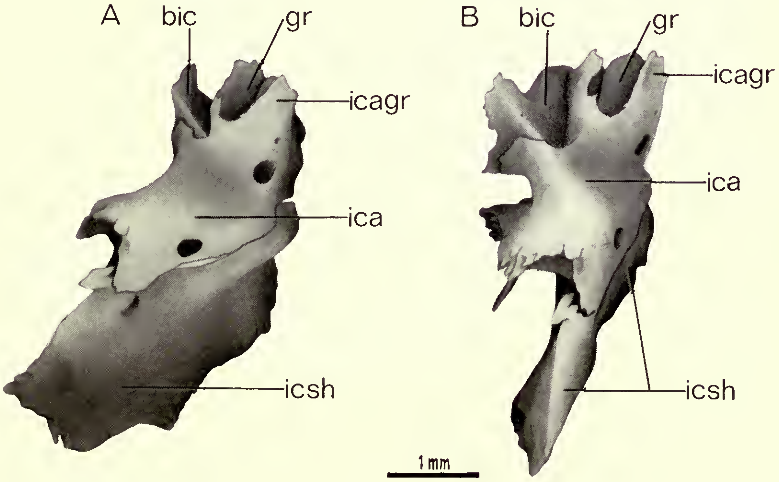
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Fig. 2

PLATE 2

Megalops cyprinoides. Posterior aspect of skull, viewed obliquely from the left side and somewhat ventrally.

Drawn by Sharon Lesure

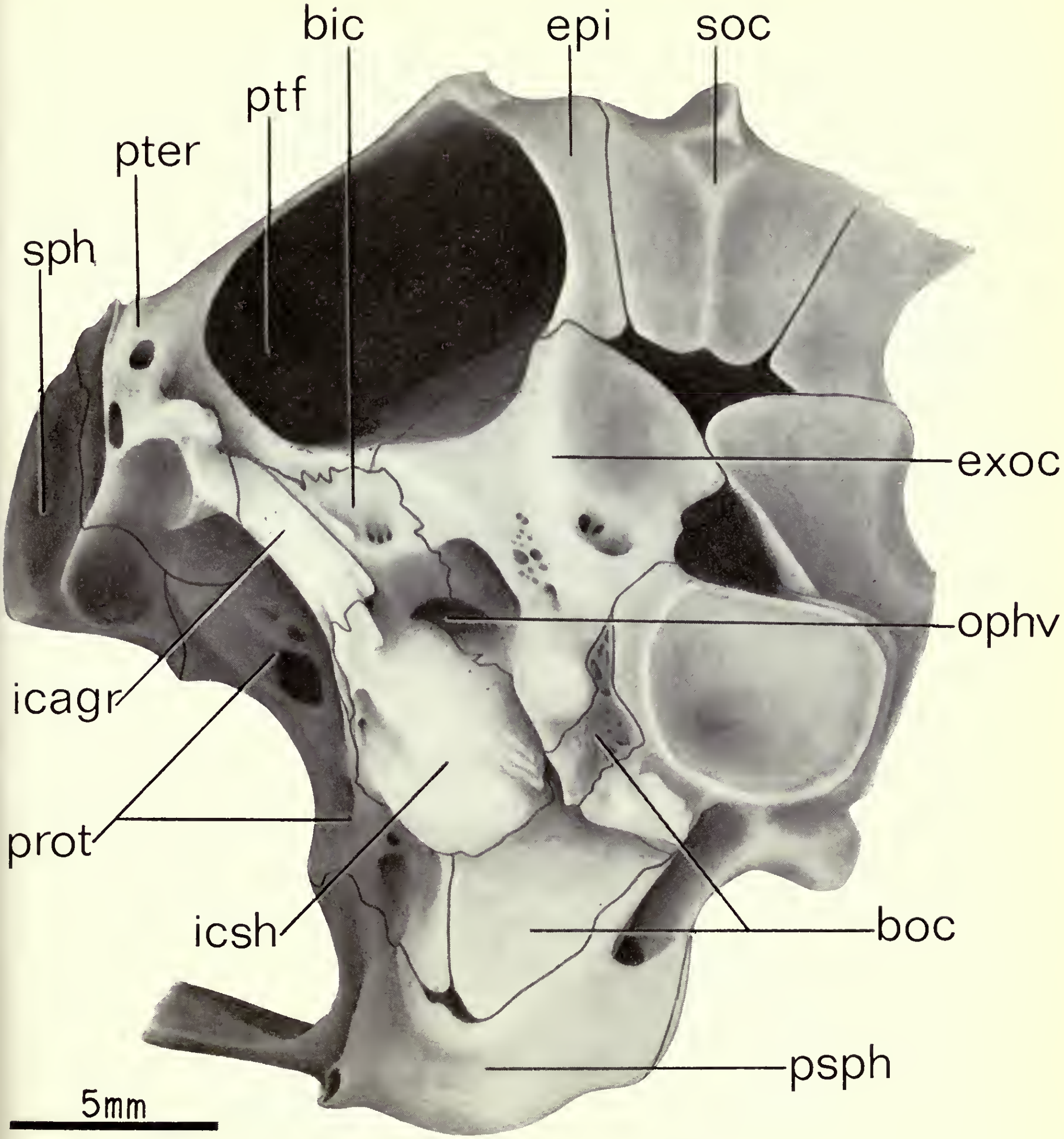
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PLATE 3

FIG. 1. *Tarpon atlanticus.* Otic region of skull (from a specimen 78·2 cms S.L.). The foramen numbered 4 is not present in the left prootic, and was absent in other specimens examined.

FIG. 2. *Tarpon atlanticus.* Intercalar and exoccipital. A, Bones orientated in their natural position but viewed obliquely from above and anteriorly. B, Bones orientated in their natural position, but viewed obliquely from above and behind. *Drawn by Sharon Lesure*

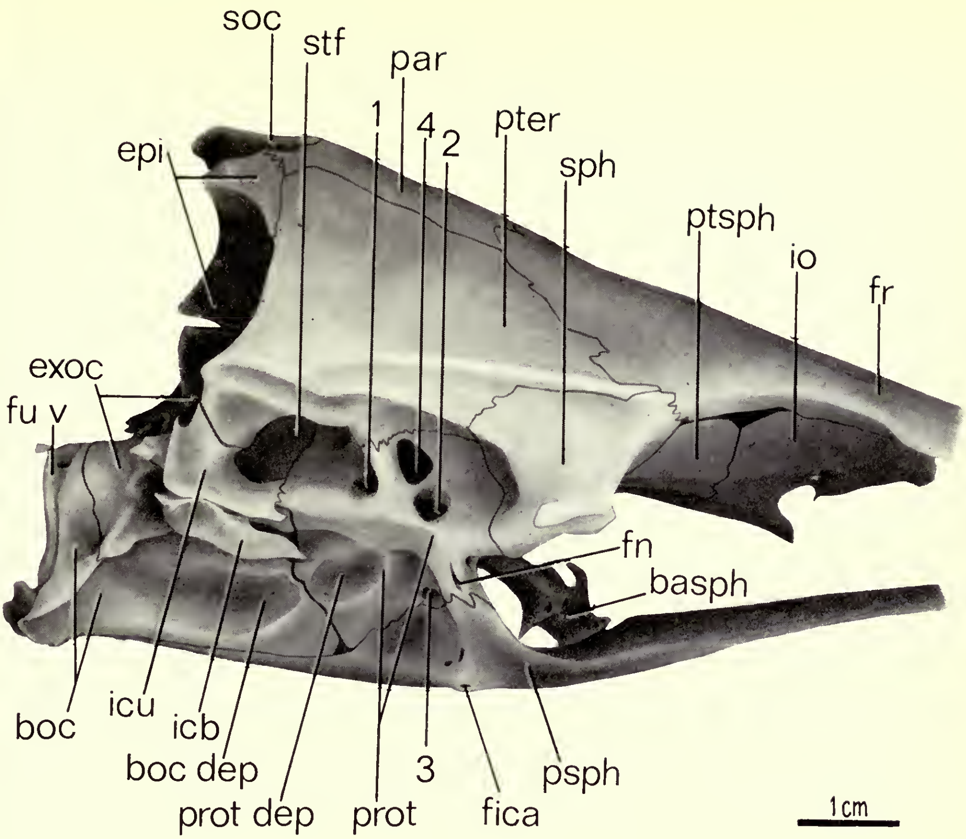
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FIG. 1

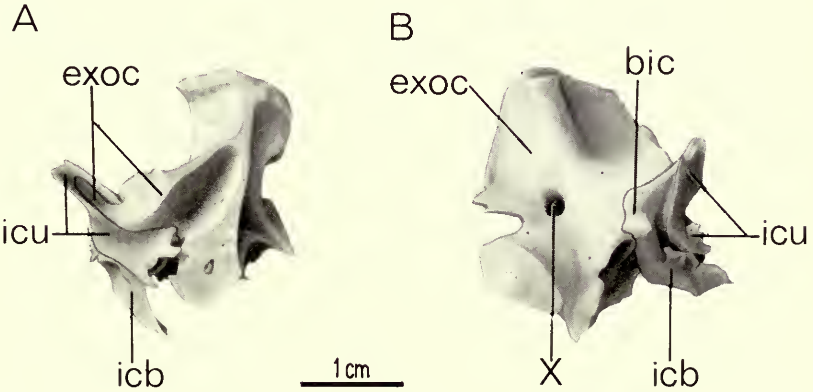
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FIG. 2

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BRITISH MUSEUM
24 APR 1970
NATURAL HISTORY

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R. M. WARWICK

BULLETIN OF
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ZOOLOGY Vol. 19 No. 4
LONDON: 1970

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24 APR 1970
NATURAL HISTORY

BY
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Department of Zoology, University of Exeter
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Pp. 137–177; 16 *Text-figures*

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TRUSTEES OF
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FOURTEEN NEW SPECIES OF FREELIVING MARINE NEMATODES FROM THE EXE ESTUARY

By R. M. WARWICK

SYNOPSIS

Fourteen new species of freeliving interstitial marine nematodes are described from sandy habitats in the Exe estuary area, South Devon. They are all referable to existing genera. *Enoplolaimus denticulatus* sp. nov. is similar to *E. connexus* Wieser, 1953, but differs from it principally in the shorter cervical setae of the female, and in the form of the spicules in the male; *Mesacanthion africanthiforme* sp. nov. is characterized by the absence of a pre-cloacal supplement, by the presence of stout post-cloacal setae in the male, and by the unique structure of the spicules and gubernaculum; *Epacanthion gorgonocephalum* sp. nov. is related to *E. enoploidiformis* (Gerlach, 1952) comb. nov. and *E. oliffi* Inglis, 1966, differing from the former in the possession of a hirsute anterior end, and from the latter in the structure of the male copulatory apparatus and in the setal arrangement on the head; *Axonolaimus orcombensis* sp. nov. is closest to *A. steineri* Timm, 1954, but differs from it in the number of subcephalic setae and in the shape of the amphids, gubernaculum and spicules; *Leptolaimus ampullaceus* sp. nov. is characterized by the number of pre-cloacal supplements, by the structure of the spicules and gubernaculum, and by the presence of longitudinal files of papillae down the body-length; *Camacolaimus barbatus* sp. nov. is closest to *C. prytherchi* Chitwood, 1935, but has shorter cephalic setae, no alae on either side of the cloaca, a prominent post-cloacal supplement, lateral papillae in the oesophageal region, and a different setal arrangement on the tail; *Paralinhomoeus uniovarium* sp. nov. is characterised by its large amphids, long cephalic setae, and by the possession of a single anterior ovary; *Theristus* (*Theristus*) *denticulatus* sp. nov. is characterized by the typically complex structure of the gubernaculum and by the presence of stout ventral spines on the male tail; *Theristus* (*Theristus*) *interstitialis* sp. nov. is characterized by its long cephalic setae, by the position and size of the amphids, and by the structure of the male copulatory apparatus; *Theristus* (*Trichotheristus*) *psammoides* sp. nov. is closest to *T.* (*T.*) *vicinus* Riemann, 1966, but has larger amphids and differently shaped spicules and gubernaculum; *Chromaspirina inglisi* sp. nov. (= *C. pontica sensu* Gerlach, 1951, *nec*. Filipjev, 1918) is characterized by a uniform covering of fine hairs over the entire body-surface; *Microlaimus spirifer* sp. nov. is characterized by the position and form of the amphids, by the form of the copulatory apparatus in the male, and by the long tail; *Pomponema reducta* sp. nov. is characterized by the possession of only six cephalic setae, and by the arrangement of denticles in the buccal cavity; *Paracanthonchus opheliae* sp. nov. is characterized by the distinctive structure of the gubernaculum and of the spicules.

INTRODUCTION

DURING the course of an ecological survey of the distribution of freeliving nematodes in the Exe estuary, several species were discovered which proved to be new. This paper deals with the species which were fairly common in the estuary, and their ecological distribution, together with that of other species, will subsequently be discussed elsewhere. Suffice it to say that all the species described here are interstitial, and were found in sandy habitats at various tide levels at Shelly Bank, just inside the mouth of the estuary at Exmouth, and on Exmouth beach near Orcombe Point.

Measurements have been made from glycerine mounts under the camera lucida with an opisometer. Curved structures, e.g., spicules, are measured as the curve and not the chord, the oesophagus length is measured from the anterior end of the body, and the head diameters are measured at the level of the first circle of cephalic setae unless otherwise stated. The type-material has been deposited at the British Museum (Natural History). The classification used is that of De Coninck (1965), but following Inglis (1966) the only groups recognized are families and genera. Where a large amount of material is available only three males and three females have been measured, since relative and absolute measurements have only a limited taxonomic value. Attention has rather been given to the morphology of the male copulatory apparatus, in response to recent pleas by Wieser and Hopper (1967) and Inglis (1967). All the species are described from a syntypic series.

Family **ENOPLIDAE**

Enoplolaimus denticulatus sp. nov.

(Fig. 1)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 262.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank: M.L.W.S.T. Orcombe Point: M.H.W.N.T., M.T.L., M.L.W.N.T.

	a	b	c	V%	Body length (mm.)
Males	52·93	4·05	19·95	—	3·97
	56·00	3·54	14·30	—	3·36
	59·22	4·12	23·11	—	3·79
Females	57·75	4·02	17·08	60·24	4·10
	51·63	4·00	21·14	62·16	4·44
	61·49	4·48	16·25	67·25	4·55

MEASUREMENTS (in mm. in order of body lengths). Males: Body breadth: 0·075; 0·060; 0·064. Oesophagus length : 0·98 ; 0·95 ; 0·92. Distance of nerve ring from anterior : 0·225 ; 0·22 ; 0·22. Head diameter : 0·053 ; 0·045 ; 0·049. Length of labial setae : 0·016 ; 0·016 ; 0·017. Length of longer cephalic setae : 0·082 ; 0·082 ; 0·071. Length of shorter cephalic setae : 0·040 ; 0·040 ; 0·032. Length of longest cervical setae : 0·043 ; 0·043 ; 0·025. Length of mandibles : 0·032 ; 0·026 : 0·027. Length of onchia : 0·019 ; 0·016 ; 0·014. Tail length : 0·199 ; 0·235 ; 0·164. Cloacal diameter : 0·050 ; 0·044 ; 0·042. Spicule length : 0·053 ; 0·060 ; 0·055. Gubernaculum length : 0·022 ; 0·020 ; 0·023. Supplement length : 0·012 ; 0·008 ; 0·011. Distance of supplement anterior to cloaca : 0·139 ; 0·144 ; 0·132.

Females : Body breadth : 0·071 ; 0·086 ; 0·074. Oesophagus length : 1·02 ; 1·11 ; 1·015. Distance of nerve ring from anterior : 0·235 ; 0·25 ; 0·235. Head diameter : 0·055 ; 0·056 ; 0·050. Length of labial setae : 0·017 ; 0·018 ; 0·017. Length of longer cephalic setae : 0·092 ; 0·070 ; 0·099. Length of shorter cephalic setae : 0·037 ; 0·029 ; 0·034. Length of longest cervical setae : 0·008 ; 0·010 ; 0·010. Length of mandibles : 0·029 ; 0·032 ; 0·029. Length of onchia : 0·019 ; 0·019 ; 0·020. Tail length : 0·24 ; 0·21 ; 0·28. Anal diameter : 0·049 ; 0·049 ; 0·051. Distance of vulva from anterior : 2·47 ; 2·76 ; 3·06.

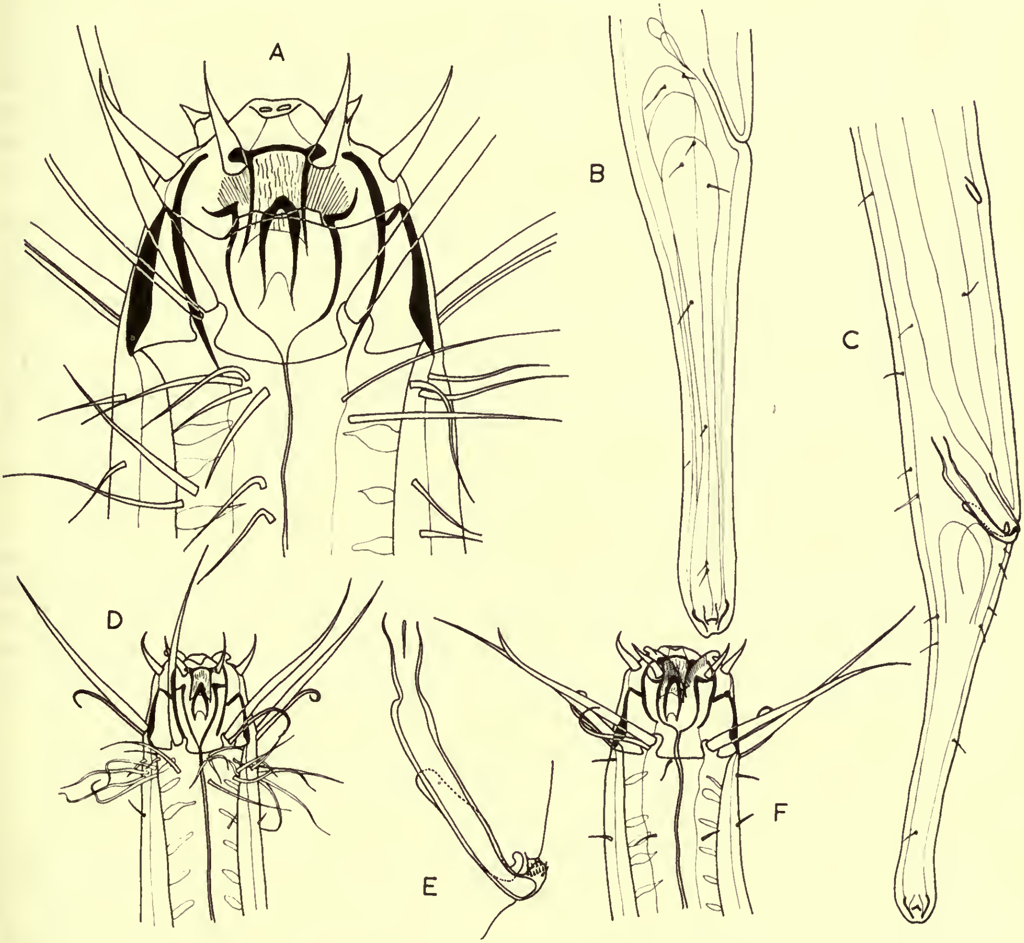


FIG. 1. *Enoplolaimus denticulatus* sp. nov. A, Details of cephalic structure of male. B, Lateral view of female tail. C, Lateral view of male tail. D, Male head. E, Lateral view of spicules and gubernaculum. F, Female head.

This is a relatively large member of the genus. The cuticle is smooth. The mouth is surrounded by three relatively high lips which have pronounced subsidiary lobes and bear semi-lunar striations on their inner surfaces (Fig. 1A). The six stout conical labial setae arise at the level of the tips of the mandibles. The six long cephalic setae are fairly stout, and the four shorter ones more slender. The posterior border of the short cephalic capsule has small incisions with fenestrae to accommodate the bases of the cephalic setae. In the male there is a series of long cervical setae just posterior to the cephalic capsule (Fig. 1D), but the female only has a circle of six very short setae in this position (Fig. 1F). The mandibles have the usual appearance of two lateral rods united by an anterior curved bar, with the pointed tips projecting into the buccal cavity. The onchia are large, and distinct from the mandibular plate. The terminology used in describing this and subsequent members of the Enoplidae follows that of Inglis (1964).

The oesophagus is cylindrical with three files of glands down its length. Short setae are fairly numerous in the oesophageal region of both sexes, but are scarce posterior to this, becoming more numerous on the tail. The proximal third of the tail is conical and the remainder cylindrical, the tip being rounded and slightly swollen (Figs. 1B and 1C)

MALE. The spicules are more or less straight when viewed laterally. The distal tips are strongly hooked and bear a series of fine denticles (Fig. 1E). The proximal ends are open and funnel shaped, and there are dorsal swellings just posterior to them. When viewed from the ventral aspect the spicules appear to be far apart proximally, bent in the middle, and closely adherent to the narrow gubernaculum in their distal half, as illustrated for *E. connexus* by Wieser (1953, p. 77, Fig. 38e). The gubernaculum is also hooked at its tip, but bears no denticles. The supplement is small, simple and tubular. The testes are paired, opposed and outstretched.

FEMALE. The ovaries are paired, opposed and doubly reflexed. They are about equal in size.

DISCUSSION. This species is closest to *E. connexus* Wieser, 1953, but differs from it in having much shorter cervical setae in the female, spicules of a different shape with denticulate tips, and the supplement in a more anterior position. The present species is much larger than *E. connexus*, and the cephalic setae are accommodated in fenestrae of the cephalic capsule and do not lie wholly posterior to it as in Wieser's species.

Mesacanthion africanthiforme sp. nov.

(Fig. 2)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 264.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.T.L., M.L.W.N.T., M.L.W.S.T. Orcombe Point : M.H.W.N.T., M.L.W.N.T.

	a	b	c	V%	Body length (mm.)
Males	81·84	5·41	19·61	—	4·49
	77·27	4·32	16·14	—	2·55
	65·83	4·09	16·01	—	2·37
Females	56·06	4·48	15·10	58·65	3·70
	57·97	4·72	21·17	61·56	3·07
	63·75	4·25	17·00	58·82	2·55

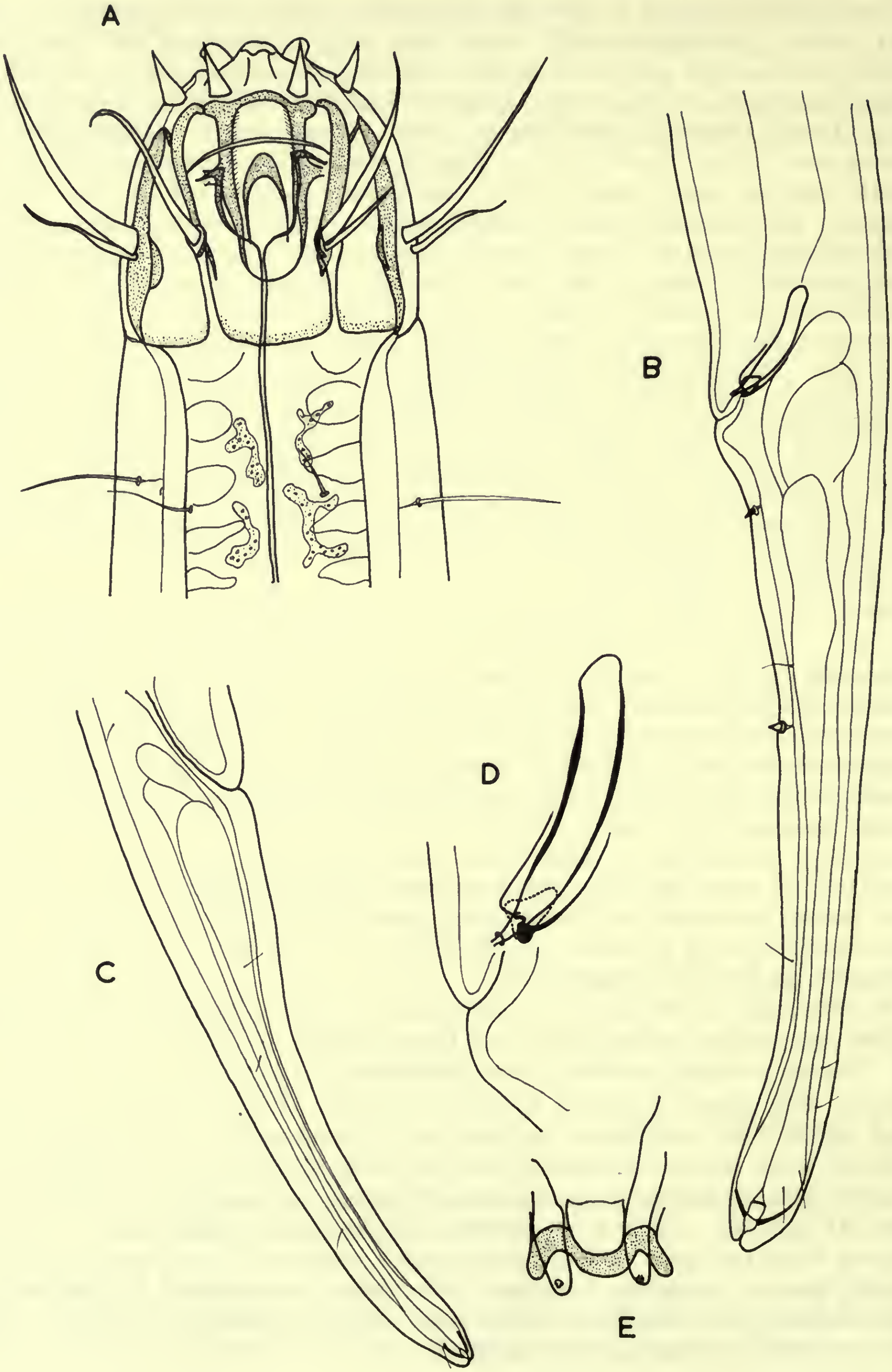
MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·055 ; 0·033 ; 0·036. Oesophagus length : 0·83 ; 0·59 ; 0·58. Distance of nerve ring from anterior : 0·24 ; 0·18 ; 0·18. Head diameter : 0.047 ; 0·032 ; 0·028. Length of labial setae : 0·008 ; 0·007 ; 0·006. Length of longer cephalic setae : 0·041 ; 0·026 ; 0·024. Length of shorter cephalic setae : 0·020 ; 0·013 ; 0·010. Length of longest cervical setae : 0·014 ; 0·016 ; 0·007. Length of mandibles : 0·029 ; 0·020 ; 0·019. Length of onchia : 0·017 ; 0·013 ; 0·012. Tail length : 0·229 ; 0·158 ; 0·148. Cloacal diameter : 0·047 ; 0·033 ; 0·033. Spicule length : 0·033 ; 0·025 ; 0·020. Gubernaculum length : 0·013 ; 0·011 ; 0·010. Distance of first pair of supplementary setae posterior to cloaca : 0·026 ; 0·014 ; 0·015. Distance of second pair of supplementary setae posterior to cloaca : 0·085 ; 0·050 ; 0·052.

Females : Body breadth : 0·066 ; 0·053 ; 0·040. Oesophagus length : 0·825 ; 0·65 ; 0·60. Distance of nerve ring from anterior : 0·26 ; 0·20 ; 0·19. Head diameter: 0·050 ; 0·036 ; 0·036. Length of labial setae : 0·007 ; 0·006 ; 0·006. Length of longer cephalic setae : 0·030; 0·023; 0·023. Length of shorter cephalic setae : 0·013 ; 0·010 ; 0·011. Length of longest cervical setae : 0·012 ; 0·010 ; 0·008. Length of mandibles : 0·032 ; 0·024 ; 0·023. Length of onchia : 0·020 ; 0·016 ; 0·014. Tail length : 0·245 ; 0·145 ; 0·150. Anal diameter : 0·045 ; 0·037 ; 0·033. Distance of vulva from anterior : 2·17 ; 1·89 ; 1·50. Egg length :— ; 0·215 ; —. Egg breadth : — ; 0·039 ; —.

This is a long slender species, and has a characteristically dome-shaped head (Fig. 2A). There are some irregular areas of pigmentation just posterior to the cephalic capsule. The cuticle is smooth. The three lips are relatively low, and have no internal striation. The six labial setae are stout and conical, and situated at the level of the tips of the mandibles. The cephalic setae originate from about the middle of the cephalic capsule, the posterior border of the capsule being deeply incised and the bases of the setae accommodated in fenestrae. The four shorter cephalic setae are about half the length of the six longer ones. There are six files of long setae extending one third to two thirds of the way down the oesophagus length in both sexes, but they tend to be more numerous in the male. Setae are scarce further posteriorly and become more numerous again in the tail region. The three mandibles have the usual appearance and bear prominent lateral processes. The onchia are large and equal in size.

The oesophagus is cylindrical, with the usual three files of glands down its length. The tail is conical in its distal third and the remainder is cylindrical (Figs. 2B and 2C). The tip is slightly swollen in some specimens.

MALE. The spicules are small and fairly straight. They are pointed and open ended distally with a thickened cuticular ring subterminally. The gubernaculum consists of a pair of tubes surrounding the distal ends of the spicules, and these tubes are united by a median bar which has a roughly triangular appearance in lateral view (Figs. 2D and 2E). There is no cuticularized pre-cloacal supplement. The tail, however, bears two pairs of stout conical setae posterior to the cloaca, and these probably have a copulatory function. This feature is parallelled in *Africanthion nudus* Inglis, 1964, which has a similar series of setae *anterior* to the cloaca. The testes are paired, opposed and outstretched.


A
B
C
D
E

FEMALE. The ovaries are paired, symmetrical, and doubly reflexed. The eggs are large and elongate.

DISCUSSION. In this species the male is distinct from all others in the combination of the absence of a pre-cloacal supplement and the presence of stout post-cloacal setae. Also the structure of the gubernaculum and spicules is unique. It is close to the genus *Africanthion* Inglis, 1964, in that the supplement is replaced by stout setae, but cannot be referred to this genus because in *Africanthion* the onchia are unequal in size, the lips have semi-lunar striations, and the copulatory setae are pre-cloacal and not post-cloacal as in the present species. Since one other species *Mesacanthion infantile* (Ditlevsen, 1930), is also reported to have no supplement, and the head structure of the present species is typical of the genus, it will be referred to *Mesacanthion.*

Epacanthion gorgonocephalum sp. nov.

(Figs. 3 and 4)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 263.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.L.W.N.T., M.L.W.S.T. Orcombe Point : M.H.W.S.T., M.H.W.N.T., M.T.L., M.L.W.N.T., M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	48·52	4·36	19·32	—	4·27
	47·44	4·38	20·53	—	4·27
	52·32	4·38	18·90	—	4·29
Females	34·86	4·58	21·38	58·84	4·81
	44·10	4·45	20·13	60·04	4·63
	37·32	4·56	20·70	60·34	4·74

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·088 ; 0·090 ; 0·082. Oesophagus length : 0·98 ; 0·975 ; 0·98. Distance of nerve ring from anterior : 0·185 ; 0·192 ; 0·190. Head diameter: 0·059 ; 0·055 ; 0·052. Length of labial setae : 0·021 ; 0·019 ; 0·022. Length of longer cephalic setae : 0·074 ; 0·063 ; 0·073. Length of shorter cephalic setae : 0·043 ; 0·042 ; 0·039. Length of longest subcephalic setae : 0·036 ; 0·037 ; 0·035. Length of shortest subcephalic setae : 0·012 ; 0·017 ; 0·011. Length of longest cervical setae : 0·048 ; 0·044 ; 0·035. Length of longest body setae : 0·029 ; 0·027 ; 0·024. Distance of dense ring of setae from anterior : 0·31 ; 0·32 ; 0·30. Mandible length : 0·020 ;

FIG. 2. *Mesacanthion africanthiforme* sp. nov. A, Male head. B, Lateral view of male tail. C, Lateral view of female tail. D, Lateral view of spicules and gubernaculum. E, Ventral view of spicules and gubernaculum.

0·019 ; 0·020. Tail length : 0·221 ; 0·208 ; 0·227. Cloacal diameter : 0·060 ; 0·057 ; 0·052. Spicule length : 0·053 ; 0·051 ; 0·050. Gubernaculum length : 0·020 ; 0·018 ; 0·018.

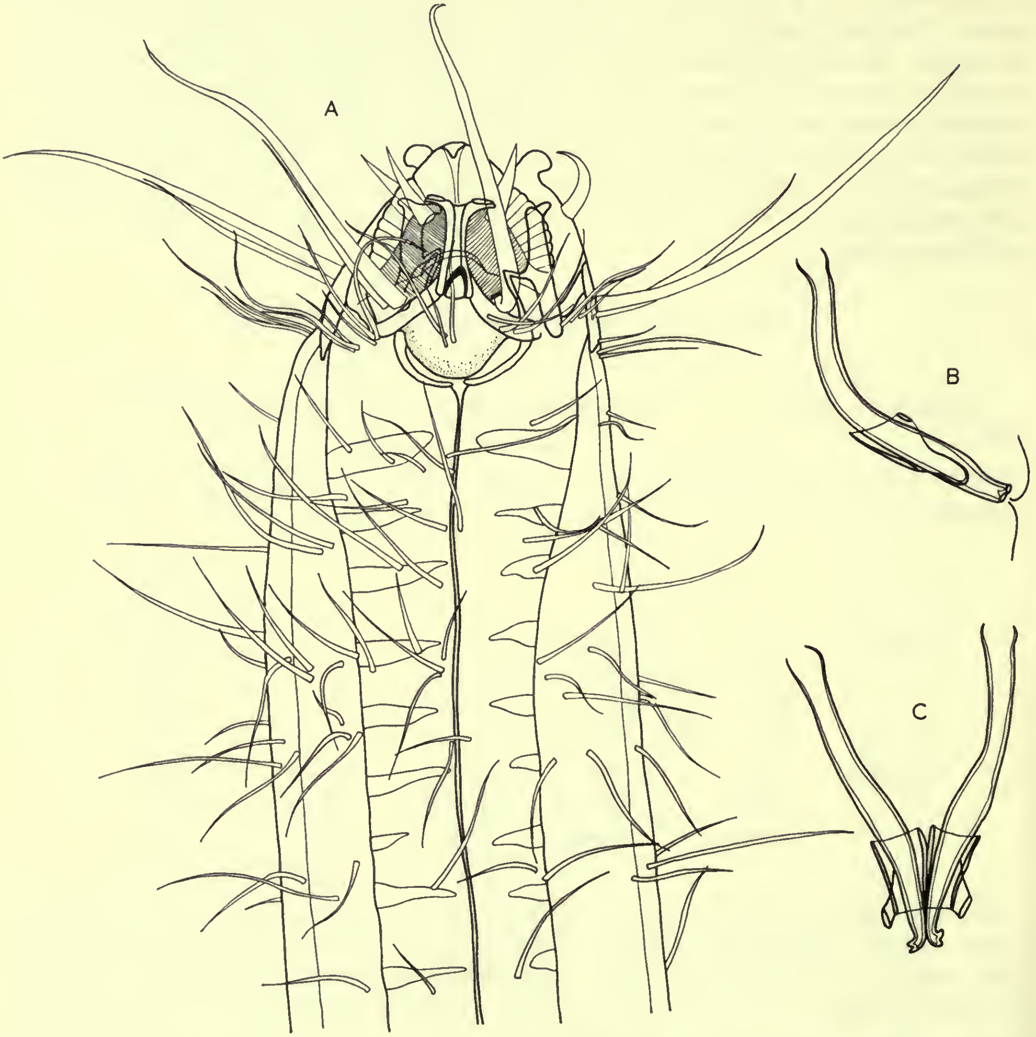


FIG. 3. *Epacanthion gorgonocephalum* sp. nov. A, Male head. B, Lateral view of spicules and gubernaculum. C, Ventral view of spicules and gubernaculum.

Females : Body breadth : 0·138 ; 0·105 ; 0·128. Oesophagus length : 1·05 ; 1·04 ; 1·04. Distance of nerve ring from anterior : 0·221 ; 0·198 ; 0·215. Head diameter : 0·059 ; 0·062 ; 0·062. Length of labial setae : 0·023 ; 0·019 ; 0·019. Length of longer cephalic setae : 0·082 ; 0·071 ; 0·073. Length of shorter cephalic setae : 0·035 ; 0·032 ; 0·034. Length of longest subcephalic setae : 0·012 ; — ; 0·011. Length of longest cervical setae : 0·028 ; 0·029 ; 0·026. Length of longest body setae : 0·023 ; 0·024 ; 0·019. Mandible length : 0·022 ; 0·019 ; 0·019. Tail length : 0·225 ; 0·230 ; 0·229. Anal diameter : 0·072 ; 0·068 ; 0·072. Distance of vulva from anterior : 2·83 ; 2·78 ; 2·86. Egg length : 0·264 ; 0·363 ; 0·312. Egg breadth : 0·113 ; 0·092 ; 0·091.

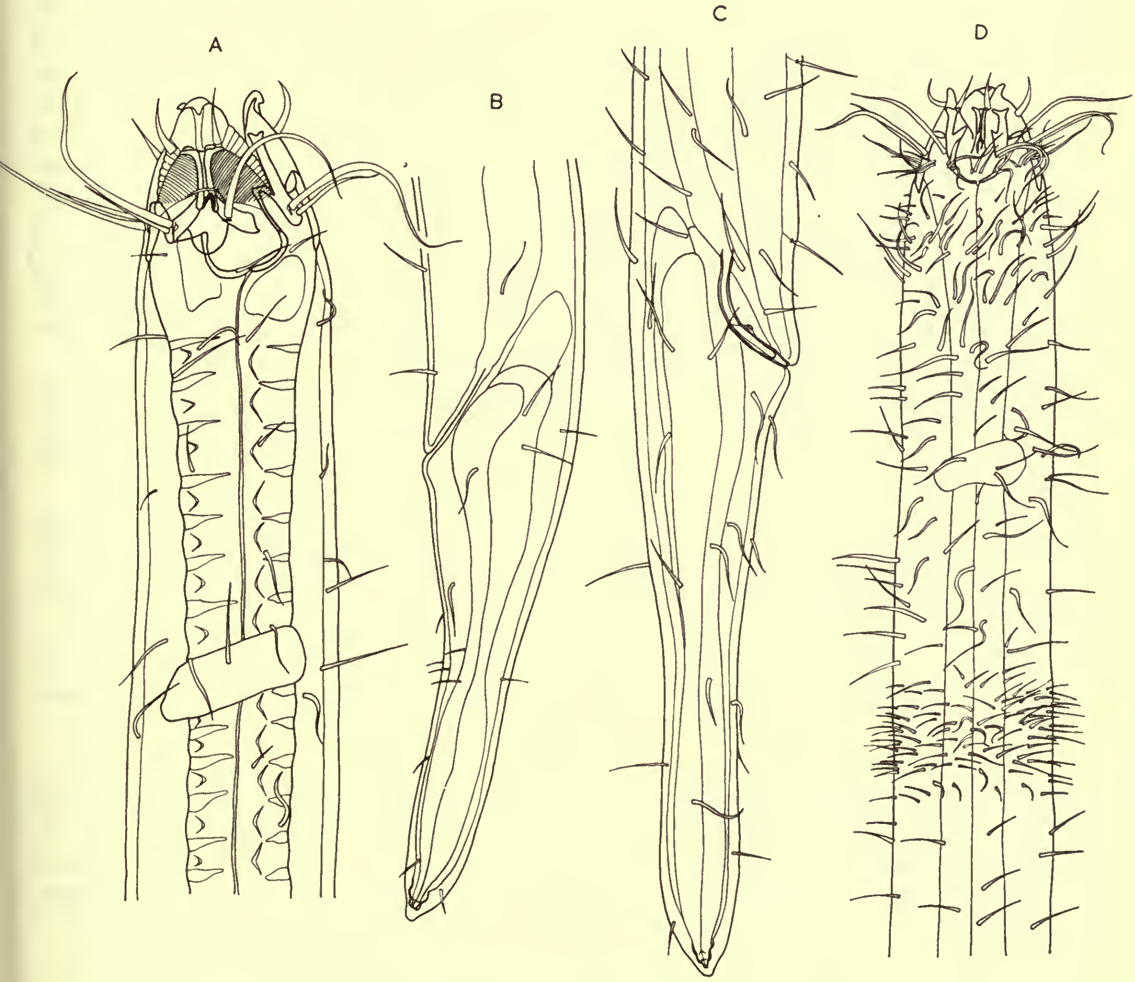


Fig. 4. *Epacanthion gorgonocephalum* sp. nov. A, Anterior end of female. B, Lateral view of female tail. C, Lateral view of male tail. D, Anterior end of male.

The body is relatively long and slender, and the cuticle smooth. The three lips have a marked subsidiary lobe, and internally are marked by semi-lunar striations posterior to a line running backwards from the tips of the mandibles. The outer parts of the lip are marked by wider spaced striations, and the lip margin is scalloped. The subsidiary lobe has no internal striation or scalloped edge (Fig. 3A). The labial setae are stout, and originate just posterior to the tips of the mandibles. There are six long and four shorter cephalic setae situated at the level of the bases of the onchia. In the male there are twelve groups of subcephalic setae, three per group, one being long, one of medium length and one short. In the female only six single short subcephalic setae are present, or these may be absent altogether (Fig. 4A). The bases of the larger cephalic setae are supported by small areas of thickened cuticle in the head. The mandibles are typical of the genus. They appear in optical section as two longitudinal rods joined by a thin sheet of cuticle, and are relatively long and slender. The three onchia are equal in size and are situated at the bases of the mandibles. The onchial plate is rounded posteriorly, and has well-developed radial processes. Each of the three plates curve inwards posteriorly, and their posterior edges almost meet at the base of the buccal cavity. The cephalic slits are prominent and crescentic, and are situated just anterior to the level of the tips of the onchia. There are numerous long dense cervical setae in the male, and there is a region of very dense, but rather shorter setae about one-third of the way down the oesophagus length (Fig. 4D). Posterior to this setae become scarcer, increasing in density again on the tail. In the female cervical setae are sparse (Fig. 4A), and there are very few setae on the body-surface until just before the anus.

The oesophagus is swollen anteriorly round the base of the buccal cavity, and is otherwise cylindrical with the usual three files of glands down its length. The anterior half of the tail is conical and the posterior half cylindrical (Figs. 4B and 4C).

MALE. The gubernaculum consists of a short double tube surrounding the ends of the spicules, and bears two small lateral projections distally (Figs. 3B and 3C). The spicules are short and slightly curved, and each bears distally a pair of laterally curving knobs. There is no pre-cloacal supplement. The testes are not visible.

FEMALE. The ovaries are paired, symmetrical, opposed and reflexed. There is usually only one egg per uterus, but one specimen was found with two in the anterior uterus.

DISCUSSION. This species is similar to *Enoplolaimus enoploidiformis* Gerlach, 1952, which should be transferred to *Epacanthion*, and also to *Epacanthion oliffi* Inglis, 1966, which both have short spicules and no pre-cloacal supplement. *E. enoploidiformis* does not have a hirsute anterior end as do *E. oliffi* and *E. gorgonocephalum*, while *E. oliffi* differs from the present species in having no gubernaculum, spicules with denticulate tips and a different setal arrangement on the head.

Family **AXONOLAIMIDAE**

Axonolaimus orcombensis sp. nov.

(Fig. 5)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 265.

DISTRIBUTION IN EXE ESTUARY. Orcombe Point : M.L.W.N.T., M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	111·07	14·81	20·73	—	3·11
	93·13	14·90	20·55	—	2·98
	113·13	15·74	21·55	—	3·62
Females	83·32	14·18	20·53	62·50	3·12
	91·43	14·55	21·92	56·25	3·20
	92·00	15·33	21·61	59·63	3·22

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·028 ; 0·032 ; 0·032. Oesophagus length : 0·21 ; 0·20 ; 0·23. Distance of nerve ring from anterior : 0·113 ; 0·120 ; 0·134. Distance of excretory pore from anterior : 0·034 ; 0·029 ; 0·036. Head diameter : 0·012 ; 0·013 ; 0·013. Length of cephalic setae : 0·023 ; 0·024 ; 0·026. Length of subcephalic setae : 0·018 ; 0·018 ; 0·017. Amphid length : 0·007 ; 0·007 ; 0·007. Amphid breadth : 0·006 ; 0·006 ; 0·006. Body diameter at level of amphids : 0·014 ; 0·015 ; 0·014. Length of buccal cavity: 0·021 ; 0·022 ; 0·024. Tail length : 0·150 ; 0·145 ; 0·168. Cloacal diameter : 0·028 ; 0·030 ; 0·031. Spicule length : 0·043 ; 0·045 ; 0·048. Gubernaculum length : 0·021 ; 0·022 ; 0·023.

Females : Body breadth : 0·037 ; 0·035 ; 0·035. Oesophagus length : 0·22 ; 0·22 ; 0·21. Distance of nerve ring from anterior : 0·132 ; 0·122 ; 0·124. Distance of excretory pore from anterior : 0·035 ; 0·032 ; 0·035. Head diameter : 0·013 ; 0·014 ; 0·014. Length of cephalic setae : 0·023 ; 0·027 ; 0·024. Length of subcephalic setae : 0·013 ; 0·018 ; 0·015. Amphid length : 0·006 ; 0·007 ; 0·006. Amphid breadth : 0·006 ; 0·006 ; 0·006. Body diameter at level of amphids : 0·016 ; 0·016 ; 0·016. Length of buccal cavity : 0·023 ; 0·023 ; 0·022. Tail length: 0·152 ; 0·146 ; 0·149. Anal diameter : 0·025 ; 0·029 ; 0·028. Distance of vulva from anterior : 1·95 ; 1·80 ; 1·92. Egg length : 0·198 ; — ; —. Egg breadth : 0·027 ; — ; —.

The body is long and slender, and the cuticle marked by fine transverse striations, which commence just behind the cephalic setae and extend almost to the tail-tip. The mouth is surrounded by six rounded lips each bearing a small conical labial papilla. There are four long cephalic setae, and in the male a circle of eight long subcephalic setae is situated just anterior to the base of the buccal cavity, while in the female the sublateral subcephalic setae are paired, giving twelve in all (Figs. 5A and 5B). The posterior portion of the buccal cavity is long and tapering, and there are no odontia in the anterior portion. The ampids are small, describing a single loop, and are almost circular in outline.

The oesophagus is cylindrical throughout its length. A few short scattered setae are present on the body-surface, particularly in the cervical region and on the tail. The tail tapers throughout its length, and in the male bears two ventrolateral files of short setae and a pair of terminal setae about 0·009 mm. long, but these are absent in the female (Figs. 5D and 5E).

MALE. The gubernaculum has a strong, irregularly-shaped, dorsally-pointing

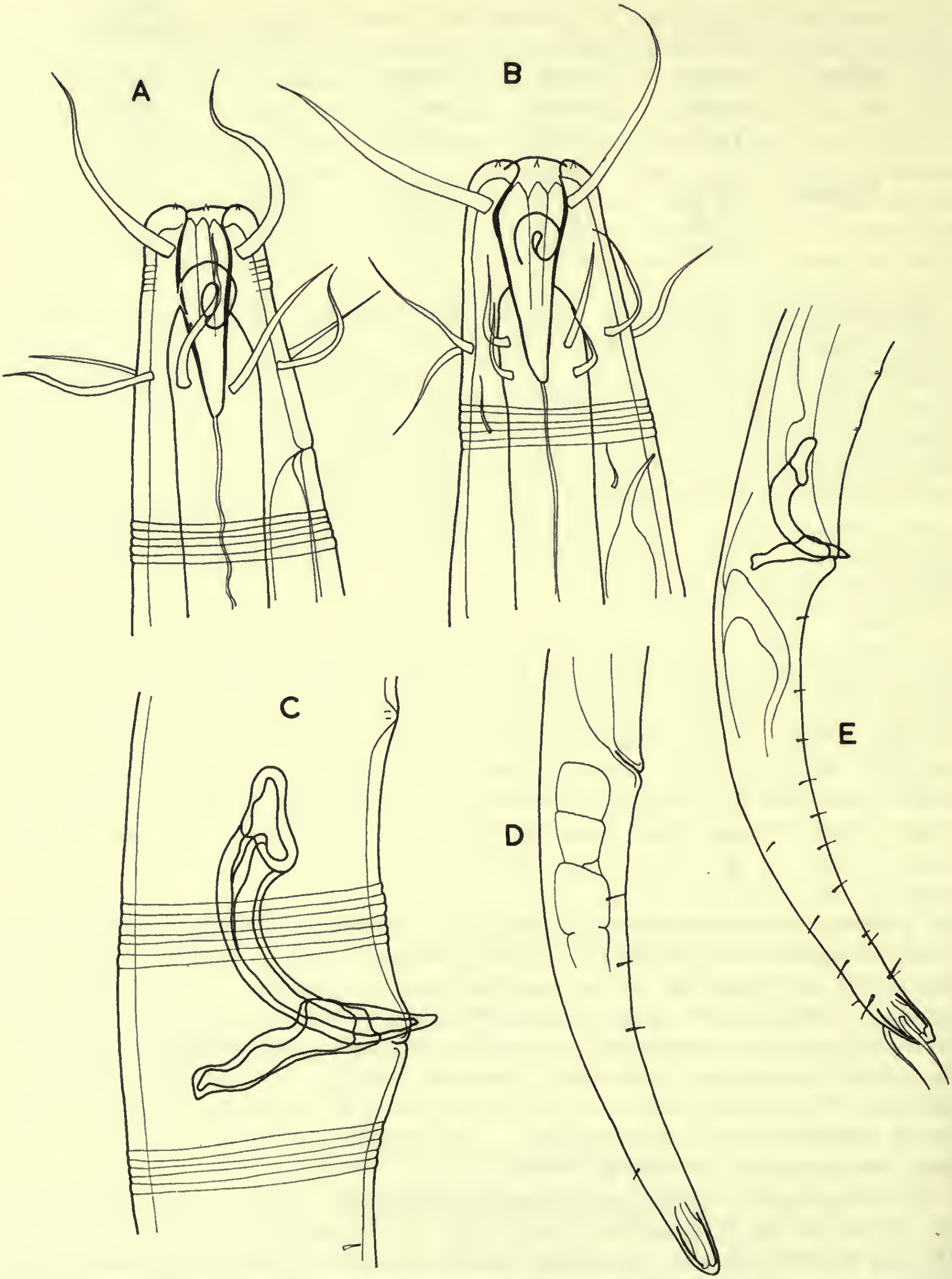


FIG. 5. *Axonolaimus orcombensis* sp. nov. A, Lateral view of male head. B, Lateral view of female head. C, Lateral view of cloacal region in male. D, Lateral view of female tail. E, Lateral view of male tail.

apophysis (Fig. 5C). The spicules are arcuate, strongly cephalate proximally and pointed distally. There are 20–30 pre-cloacal supplements, more widely spaced posteriorly than anteriorly. Each consists of a small pore, and between them the ventral body-cuticle is markedly thickened. The testes are paired, opposed and outstretched.

FEMALE. The ovaries are paired, symmetrical, opposed and reflexed. The eggs are very large and elongate.

DISCUSSION. The only other species with cephalic setae approaching two head diameters in length and with amphids which do not reach the level of the base of the buccal cavity is *A. steineri* Timm, 1954. *A. orcombensis* differs from this species in the number of subcephalic setae, in the shape of the amphids, in the form of the gubernaculum and spicules and in the general body proportions.

Family **LEPTOLAIMIDAE**

Leptolaimus ampullaceus sp. nov.

(Fig. 6)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 266.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.T.L., M.L.W.N.T., M.L.W.S.T. Orcombe Point : M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	61·43	7·05	7·17	—	0·86
	58·67	6·93	6·52	—	0·88
	67·87	8·48	7·04	—	0·95
Females	45·52	7·17	7·76	48·49	1·32
	61·18	7·70	6·62	46·15	1·04
	51·76	6·98	6·29	48·86	0·88

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth: 0·014 ; 0·015 ; 0·014. Oesophagus length : 0·122; 0·127 ; 0·112. Distance of nerve ring from anterior : 0·075 ; 0·080 ; 0·178. Head diameter : 0·004 ; 0·005 ;0 0·05. Length of cephalic setae : 0·005 ; 0·006 ; 0·005. Amphid breadth : 0·005 ; 0·005 ; 0·005. Amphid length : 0·006 ; 0·007 ; 0·006. Body diameter at level of amphids : 0·007 ; 0·008 ; 0·008. Tail length : 0·120 ; 0·135 ; 0·135. Cloacal diameter : 0·014 ; 0·015 ; 0·014. Spicule length : 0·017 ; 0·018 ; 0·019. Gubernaculum length : 0·009 ; 0·009 ; 0·009. Supplement length : 0·010 ; 0·011 ; 0·010.

Females : Body breadth : 0·029 ; 0·017 ; 0·017. Oesophagus length : 0·184 ; 0·135 ; 0·126. Distance of nerve ring from anterior : 0·111 ; 0·094 ; 0·083. Head diameter : 0·007 ; 0·007 ; 0·005. Length of cephalic setae : 0·008 ; 0·007 ; 0·005.

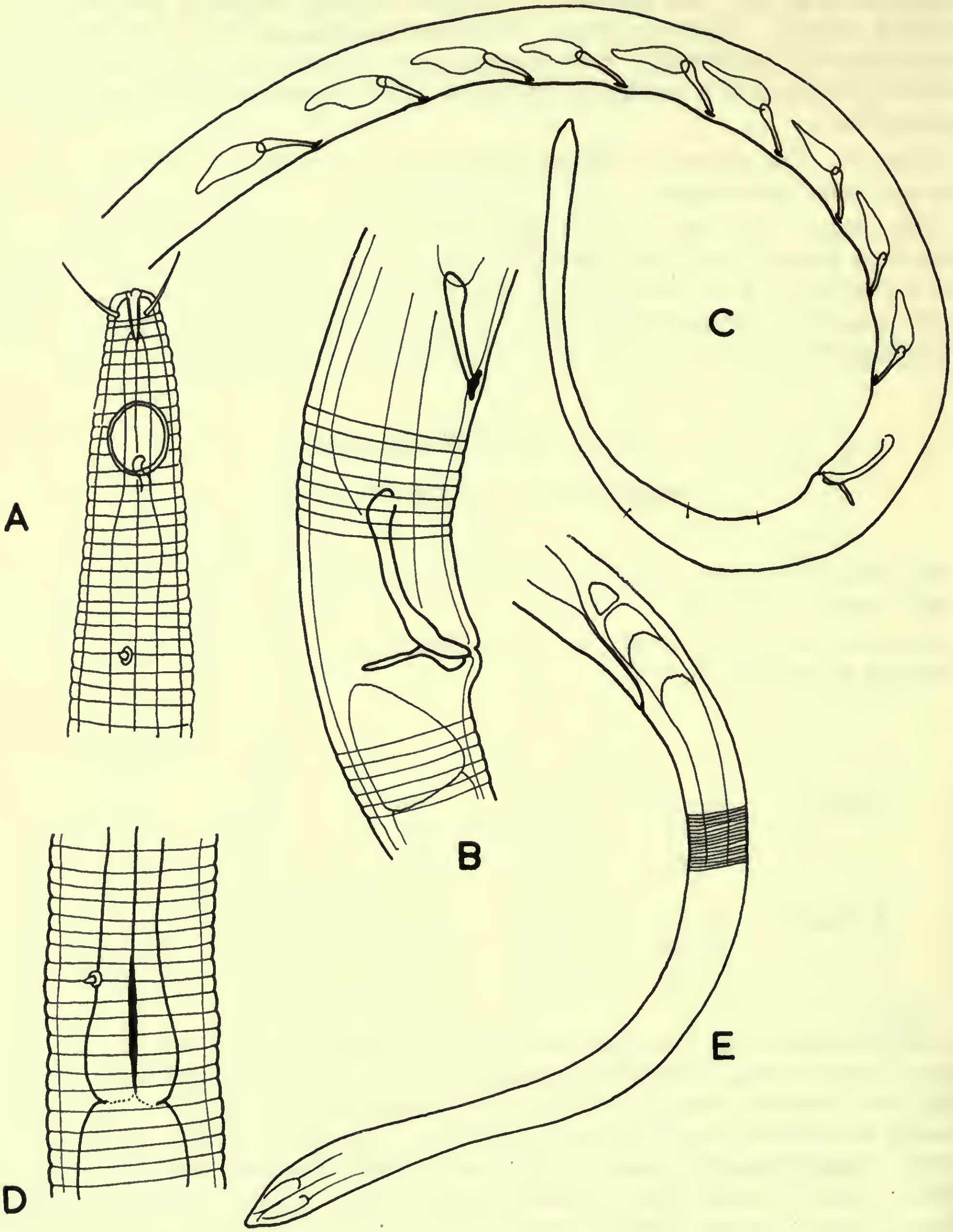


Fig. 6. *Leptolaimus ampullaceus* sp. nov. A, Lateral view of male head. B, Lateral view of cloacal region in male. C, Lateral view of posterior end of male. D, Region of oesophageal bulb. E, Lateral view of female tail.

Amphid breadth : 0·005 ; 0·004 ; 0·004. Amphid length : 0·006 ; 0·005 ; 0·004. Body diameter at level of amphids : 0·009 ; 0·008 ; 0·007. Tail length : 0·170 ; 0·157 ; 0·140. Anal diameter : 0·015 ; 0·013 ; 0·010. Distance of vulva from anterior : 0·64 ; 0·48 ; 0·43. Egg length : 0·066 ; — ; —. Egg breadth : 0·015 ; — ; —.

Transverse striation of the cuticle extends from the level of the cephalic setae to the tip of the tail. There is no lateral differentiation, but a single file of prominent conical papillae is present down each side of the body. The lips are indistinct and no labial papillae can be seen. Four long cephalic setae are present. The buccal cavity appears to be small and conical (Fig. 6A), but merges imperceptibly with the lumen of the oesophagus and may possibly be long and tubular as in other members of the genus. The amphids are large, and oval in outline. The amphidial nerve is prominent, and exits posteriorly. The amphids are slightly larger in the male than in the female. The oesophagus is narrow at its anterior end and broadens just posterior to the amphids. It has three small swellings along its length, and terminates in a small bulb (Fig. 6D). The long tail is more or less cylindrical in the female, but in the male the first third is conical and the posterior two-thirds filiform (Figs. 6C & 6E). There are a few scattered setae on the male tail.

MALE. The gubernaculum is small, and bears a pair of dorsal apophyses which are relatively slender (Fig. 6B). The spicules are dilated distally, with pointed tips, and become narrow proximally with cephalate ends. There are 7–9 tubular well-cuticularized pre-cloacal supplements, each being cephalate proximally and attached to a pear-shaped ampulla. Distally they pass through a small densely-thickened area of body-cuticle. The testes are paired, opposed and outstretched.

FEMALE. The ovaries are paired, symmetrical, opposed and outstretched. The eggs are large and elongate. In the third female measured above there is a single ventral supplement identical in structure to those found in the male. It is situated 0·170 mm. posterior to the vulva.

DISCUSSION. This species is probably closest to *L. setiger* Schuurmans Stekhoven & De Coninck, 1933, the males of which are described by Gerlach (1952). It differs from this species in the number of pre-cloacal supplements (16 in *L. setiger*), in the structure of the gubernaculum and spicules, and in the presence of lateral files of papillae down the body-length. There may also be a difference in the structure of the buccal cavity but, as mentioned above, this feature is difficult to interpret in the present specimens.

Family **CAMACOLAIMIDAE**

Camacolaimus barbatus sp. nov.

(Fig. 7)

MATERIAL STUDIED. Two males and one female. B.M. (N.H.), Reg. No. 1968. 267.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.H.W.N.T., M.T.L., M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	51·84	7·30	21·18	—	1·97
	50·25	7·44	21·85	—	2·01
Female	48·11	6·85	21·71	52·25	1·78

Measurements (in mm. in order of body lengths). Males : Body breadth : 0·038 ; 0·040. Oesophagus length : 0·27 ; 0·27. Distance of nerve ring from anterior : 0·122 ; 0·148. Head diameter : 0·011 ; 0·011. Length of cephalic setae : 0·003 ; 0·003. Amphid width : 0·005 ; 0·004. Length of buccal tooth : 0·029 ; 0·029. Tail length : 0·093 ; 0·092. Cloacal diameter : 0·031 ; 0·032. Spicule length : 0·058 ; 0·053. Gubernaculum length : 0·016 ; 0·015.

Female : Body breadth : 0·037. Oesophagus length : 0·26. Distance of nerve ring from anterior : 0·153. Head diameter : 0·012. Length of cephalic setae : 0·003. Amphid width : 0·005. Length of buccal tooth : 0·032. Tail length : 0·082. Anal diameter : 0·028. Distance of vulva from anterior : 0·93.

Coarse transverse striations of the cuticle commence just posterior to the cephalic setae and extend to a level just anterior to the spinerette on the tail-tip. Two lateral longitudinal lines indicate narrow fields of unstriated cuticle, and can first be detected a short distance behind the base of the oesophagus. They fade out just posterior to the anus or cloaca. There is a lateral file of small conical papillae between the head and the base of the oesophagus, but otherwise the body is naked.

The lips are indistinct, and there are six small conical labial papillae. The four cephalic setae are very short. The dorsal buccal tooth has a prominent shoulder near its distal tip where it leaves the oesophageal musculature (Fig. 7B). The distal tip of the tooth is rounded, and proximally it extends far down into the lumen of the oesophagus. The amphids are positioned just anterior to the cephalic setae. They are more or less circular, with the amphidial nerve extremely prominent and attached to the dorsal side of the amphid. The anterior four-fifths of the oesophagus is narrow and cylindrical, with three small swellings down its length. The posterior fifth is conical, giving the oesophagus a broad base. The tail is conical, with a pointed unstriated spinerette (Figs. 7A and 7C).

Male. The gubernaculum is small, with pointed apophyses projecting dorsally on both the dorsal and ventral sides of the spicule tips (Fig. 7C). The spicules are bent in the middle, with the proximal half swollen and the distal half narrow. Proximally they terminate in sharp right-angle bends so that the tips point ventrally. There is a pair of stout conical setae just posterior to the cloaca. A large ventral post-cloacal supplement is present one quarter of the tail-length from the tail tip. It consists of a circular area of thin cuticle by which the epidermis communicates by a protoplasmic thread with the exterior. On either side of the supplement is a stout conical seta, and there is another pair of setae positioned more laterally between the supplement and tail-tip. The testes are paired, opposed and outstretched.

Female. The ovaries are paired, symmetrical, opposed and reflexed.

Discussion. This species is closest to *C. prytherchi* Chitwood, 1935, but differs from it in having much shorter cephalic setae (3μ as compared with $8–10\mu$), no alae on either side of the cloaca, and in having a prominent post-cloacal supplement. *C. prytherchi* has only one pair of setae on the male tail (the pair immediately posterior to the cloaca), and has no lateral papillae in the oesophageal region. *C. prytherchi* has been redescribed by Wieser and Hopper (1967), and it is with this description that

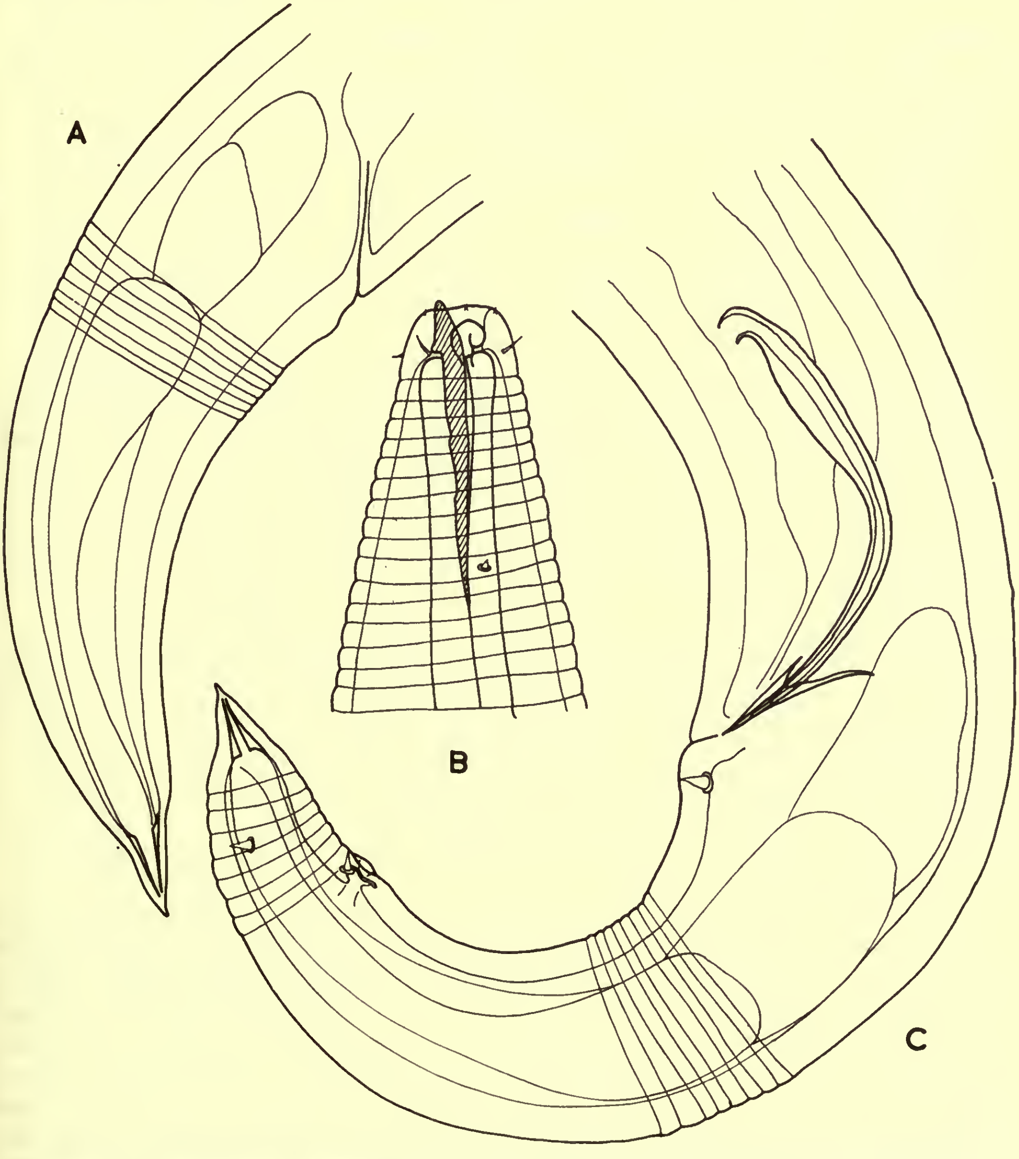


Fig. 7. *Camacolaimus barbatus* sp. nov. a, Lateral view of female tail. b, Lateral view of male head. c, Lateral view of male tail.

the present species is compared since these authors, in re-examining the type-specimen, have found structures not originally described by Chitwood.

Family **LINHOMOEIDAE**

Paralinhomoeus uniovarium sp. nov.

(Fig. 8)

MATERIAL STUDIED. One male and two females. B.M. (N.H.), Reg. No. 1968. 268.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank: M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Male	64·38	16·75	14·11	—	2·06
Females	61·30	16·79	15·84	59·22	2·82
	53·58	17·75	13·33	59·51	2·84

MEASUREMENTS (in mm. in order of body lengths). Male : Body breadth : 0·032. Oesophagus length : 0·123. Distance of nerve ring from anterior : 0·084. Distance of excretory pore from anterior : 0·072. Head diameter : 0·018. Length of longer cephalic setae : 0·018. Length of shorter cephalic setae : 0·013. Length of cervical setae : 0·007. Amphid length : 0·016. Amphid breadth : 0·013. Body diameter at level of amphids : 0·018. Distance of amphids from anterior : 0·011. Tail length : 0·146. Cloacal diameter : 0·021. Spicule length : 0·023. Gubernaculum length : 0·012.

Females : Body breadth : 0·046 ; 0·053. Oesophagus length : 0·168 ; 0·160. Distance of nerve ring from anterior : 0·097 ; 0·098. Distance of excretory pore from anterior : 0·088 ; 0·084. Head diameter : 0·027 ; 0·020. Length of longer cephalic setae : 0·019 ; 0·018. Length of shorter cephalic setae : 0·012 ; 0·012. Length of cervical setae : 0·005 ; 0·007. Amphid length : 0·017 ; 0·017. Amphid breadth : 0·013 ; 0·014. Body diameter at level of amphids : 0·025 ; 0·024. Distance of amphids from anterior : 0·013 ; 0·013. Tail length : 0·178 ; 0·213. Anal diameter : 0·023 ; 0·023. Distance of vulva from anterior : 1·67 ; 1·69. Egg length : — ; 0·142. Egg breadth : — ; 0·041.

The body is long and slender. The cuticle is marked by fine transverse striations commencing at the level of the amphids and extending almost to the tail-tip. The mouth is surrounded by six low lips each bearing a small conical labial papilla. There are four long cephalic setae and six shorter ones. In the male the cervical setae commence well anterior on the body, and what appears to be a pair of lateral cephalic setae in Fig. 8A is in fact one cephalic and one cervical seta. The buccal cavity is cyathiform and rather weakly cuticularized (Figs. 8A and 8B). The amphids are slightly subcircular, elongate longitudinally, and are broken at the base for the exit of the amphidial nerve. They are concave, but have a circular raised region in the centre.

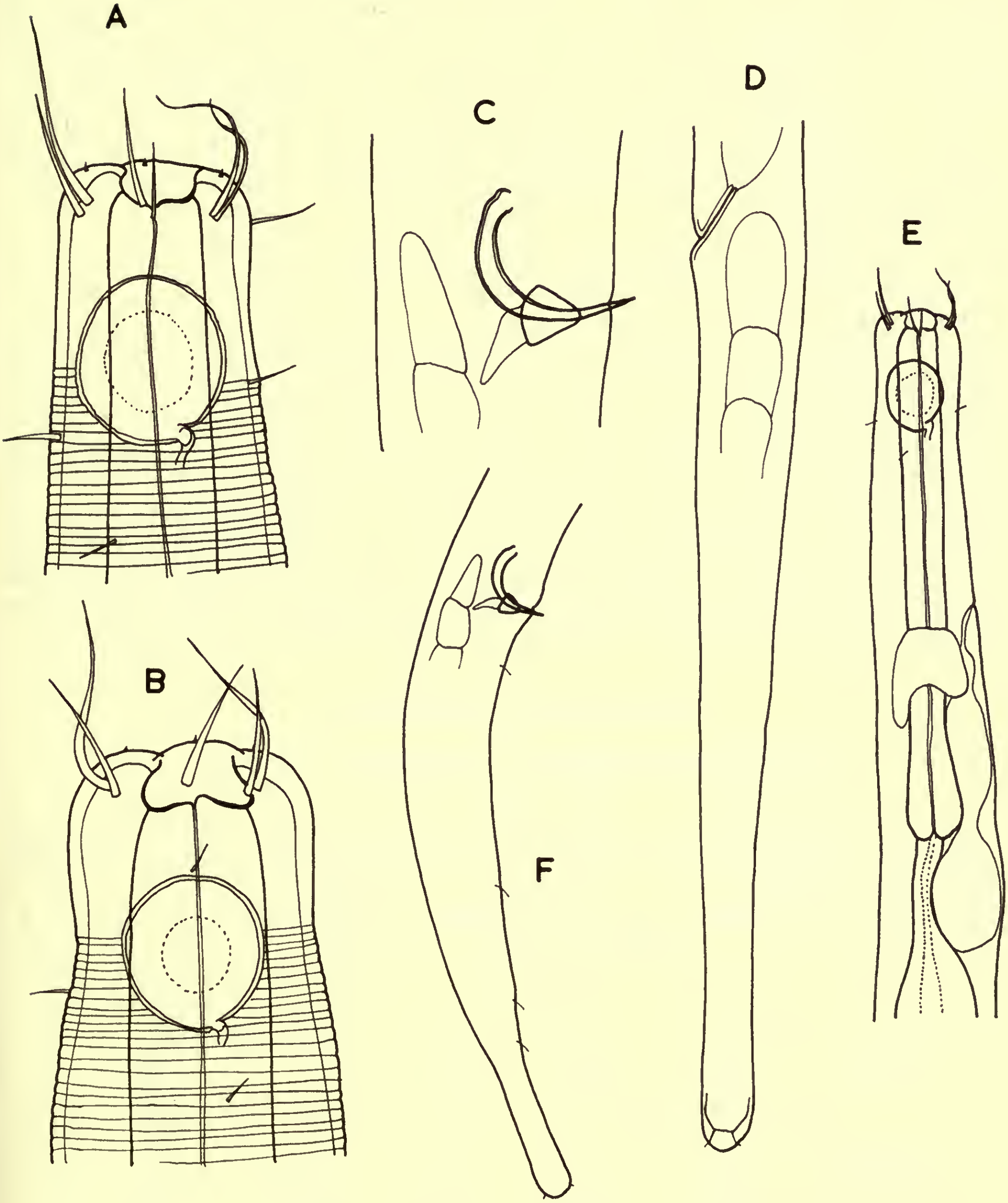


FIG. 8. *Paralinhomoeus uniovarium* sp. nov. A, Lateral view of male head. B, Lateral view of female head. C, Lateral view of spicules and gubernaculum. D, Lateral view of female tail. E, Anterior end of male. F, Lateral view of male tail.

The oesophagus is slightly swollen at its base (Fig. 8E), and the ventral gland extends just beyond this swelling. There are a few scattered setae in the cervical region, and on the male tail, but otherwise the body is naked. The tail is long, and in the male the proximal three-quarters is tapering and the distal quarter cylindrical (Fig. 8F). The female tail is more evenly tapered down its entire length (Fig. 8D).

MALE. The gubernaculum is roughly triangular in lateral view, with a pair of weakly-cuticularized postero-dorsal apophyses (Fig. 8C). The spicules are short and strongly arcuate, very slightly cephalate proximally and pointed distally. The testes are not visible.

FEMALE. There is a single long anterior outstretched ovary, and the posterior one is reduced to a small post-vulvular sac.

DISCUSSION. Species are known from this genus both with paired and single ovaries. However, a division of the genus on this basis cannot be made at the present time since the form of the female reproductive system has not been noted in all species descriptions, and cannot always be inferred from the position of the vulva alone. Further, some species are described from males only. The present species is in many respects intermediate between *Paralinhomoeus* de Man, 1907, and *Halinema* Cobb, 1920. It has large amphids with a central raised portion, as in *Halinema*, but the cephalic setae are shorter and there are neither subventral rows of conoid appendages nor long terminal setae on the male tail. *Paralinhomoeus uniovarium* is distinguished from other members of the genus by the form and size of the amphids, by the length of the cephalic setae and by the shape of the tail.

Family **MONHYSTERIDAE**

Theristus (Theristus) denticulatus sp. nov.

(Fig. 9)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 269.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.T.L., M.L.W.N.T., M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	23·14	4·05	7·17	—	0·81
	28·00	4·41	6·91	—	0·56
	25·91	4·22	6·71	—	0·57
Females	26·67	4·28	6·78	57·50	0·80
	22·92	4·20	7·05	60·00	0·55
	21·85	4·31	7·11	57·61	0·59

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·035 ; 0·020 ; 0·022. Oesophagus length : 0·200 ; 0·127 ; 0·135. Distance of nerve

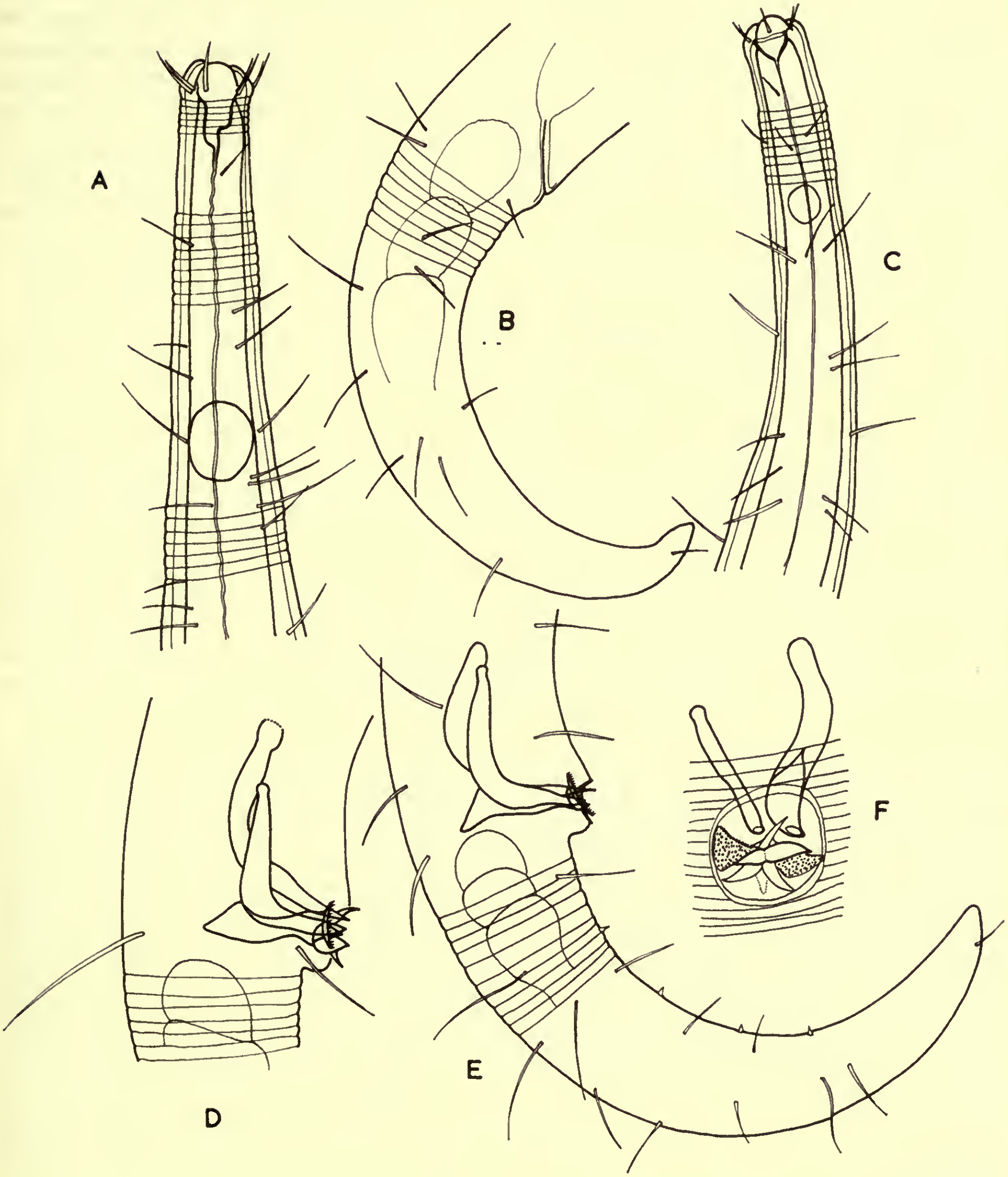


Fig. 9. *Theristus* (*Theristus*) *denticulatus* sp. nov. A, Lateral view of male head. B, Lateral view of female tail. C, Lateral view of female head. D, Lateral view of cloacal region in male. E, Lateral view of tail of another male. F, Ventral view of male cloacal region.

ring from anterior : 0·123 ; 0·073 ; 0·079. Head diameter : 0·009 ; 0·007 ; 0·007. Length of cephalic setae : 0·007 ; 0·004 ; 0·004. Length of longest cervical setae : 0·023 ; 0·012 ; 0·015. Amphid width : 0·008 ; 0·005 ; 0·005. Body diameter at level of amphids : 0·013 ; 0·008 ; 0·008. Distance of amphids from anterior : 0·042 ; 0·017 ; 0·021. Tail length : 0·113 ; 0·081 ; 0·085. Cloacal diameter : 0·026 ; 0·020 ; 0·022. Length of right spicule : 0·026 ; 0·025 ; 0·026. Length of left spicule : 0·032 ; 0·032; 0·032. Gubernaculum length : 0·017 ; 0·015 ; 0·017.

Females : Body breadth : 0·030 ; 0·024 ; 0·027. Oesophagus length : 0·187 ; 0·131 ; 0·137. Distance of nerve ring from anterior : 0·107 ; 0·080 ; 0·079. Head diameter : 0·011 ; 0·007 ; 0·008. Length of cephalic setae : 0·006 ; 0·003 ; 0·004. Length of longest cervical setae : 0·008 ; 0·013 ; 0·012. Amphid width : 0·005 ; 0·004 ; 0·005 ; Body diameter at level of amphids : 0·012 ; 0·009 ; 0·008. Distance of amphids from anterior : 0·022 ; 0·022 ; 0·021. Tail length : 0·118 ; 0·078 ; 0·083. Anal diameter : 0·022 ; 0·019 ; 0·017. Distance of vulva from anterior : 0·46 ; 0·33 ; 0·34. Egg length : — ; — ; 0·042. Egg breadth : — ; — ; 0·021.

The head end is attenuated considerably from a point about half-way down the oesophagus-length. There are ten cephalic setae, and the submedian pairs are only slightly subequal in length. The labial sense organs are not detectable. The structure of the buccal cavity is typical of the genus. The amphids are slightly subcircular and elongated longitudinally. They are situated well posterior on the body, although their position is somewhat variable (Figs. 9A & 9C). The oesophagus broadens considerably towards its posterior end in association with the attenuation of the neck region. Longish setae, up to about three-quarters of the body-width, are scattered over the entire body-surface. The tail is conical (Figs. 9B and 9E).

MALE. At the distal end of the gubernaculum is a complex array of structures. There are two flat lateral plates which are triangular when viewed from the ventral aspect, and covered ventrally with minute denticles. In a more median position there is a pair of laterally-curving points, and also three more slender points, one passing anteriorly between the distal tips of the spicules and the other two pointing posterolaterally (Figs. 9D, 9E & 9F). Proximally the gubernaculum bears a short triangular dorsally, or slightly posterodorsally, pointing apophysis. The spicules are unequal in size and structure. The right one is the shorter and is sharply bent in the middle with a narrow rounded slightly cephalate proximal tip and a pointed distal tip. The left spicule is less sharply bent. There is a file of stout conical spines arranged ventrally down the length of the tail. The structure of the gonads is not clear.

FEMALE. There is a single pre-vulvular outstretched ovary and a small post-vulvular sac.

DISCUSSION. The size of the body, position of amphids, etc., are so variable in this species that at first more than one species was thought to be present. However, the measurements and fine structure of the various parts of the male copulatory apparatus proved to be so constant that the specimens are considered monospecific. It is probable, therefore, that the position and size of the amphids are of little value in delimiting species among the homogeneous group of species to which *T. denticulatus* belongs. This group contains species of the subgenus *Theristus* with unequal spicules and comprises *T. heterospiculum* Allgén, 1932, *T. heterospiculoides* Gerlach, 1952, *T. diversispiculum* Gerlach, 1953, *T. asymetricus* (Wieser, 1956), *T. wimmeri* Wieser, 1959, *T. rhynchonemoides* Hopper, 1961, and *T. roscoffiensis* Vitiello, 1967. *T. problematica* (Allgén, 1927) is a doubtful species, and Wieser's (1956) redescription has been named by Vitiello (1967) as *T. asymetricus*. The present specimens differ from all these species in the complex structure of the gubernaculum and the ventral spines on the male tail.

Theristus (Theristus) interstitialis sp. nov.

(Fig. 10)

MATERIAL STUDIED. Three males. B.M. (N.H.), Reg. No. 1968. 270.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.H.W.S.T., M.L.W.N.T. Orcombe Point : M.L.W.S.T.

	a	b	c	Body length (mm.)
Males	55·00	6·53	9·79	1·43
	53·33	6·32	9·66	1·44
	51·11	6·19	9·65	1·38

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·026 ; 0·027 ; 0·027. Oesophagus length : 0·219 ; 0·228 ; 0·223. Distance of nerve ring from anterior : 0·112 ; 0·102 ; 0·120. Head diameter : 0·021 ; 0·018; 0·019. Length of long cephalic setae : 0·021 ; 0·019 ; 0·019. Length of medium cephalic setae : 0·017 ; 0·017 ; 0·017. Length of short cephalic setae : 0·008 ; 0·007 ; 0·009. Amphid diameter : 0·009 ; 0·010 ; 0·009. Body diameter at level of amphids : 0·024 ; 0·022 ; 0·023. Distance of amphids from anterior : 0·016 ; 0·012 ; 0·017. Tail length : 0·146 ; 0·149 ; 0·143. Cloacal diameter : 0·026 ; 0·027 ; 0·027. Spicule length : 0·042 ; 0·039 ; 0·039. Gubernaculum length : 0·081 ; 0·017 ; 0·016.

The cuticle is fairly coarsely striated. The labial setae are prominent and conical, 5μ in length. There are 14 cephalic setae, the submedian pairs being only slightly subequal and the lateral triplets having an additional much shorter seta (Fig. 10A). Body setae are sparse, short and scattered, becoming more numerous on the tail. The buccal cavity and amphids are typical of the genus in structure. The oesophagus is more or less cylindrical throughout its length. The tail is conical (Fig. 10C).

MALE. The gubernaculum has a pair of short rounded caudo-dorsal apophyses proximally, and a pair of lateral projections distally which are each tipped with two teeth (Figs. 10B and 10D). The spicules are paired and equal, strongly cephalate proximally, but distally obscured by the gubernaculum.

Discussion. This species belongs to group B.2. in the key of Wieser (1956), and is distinguished from other members of the group by the long cephalic setae, by the position and size of the amphids and by the structure of the male copulatory apparatus.

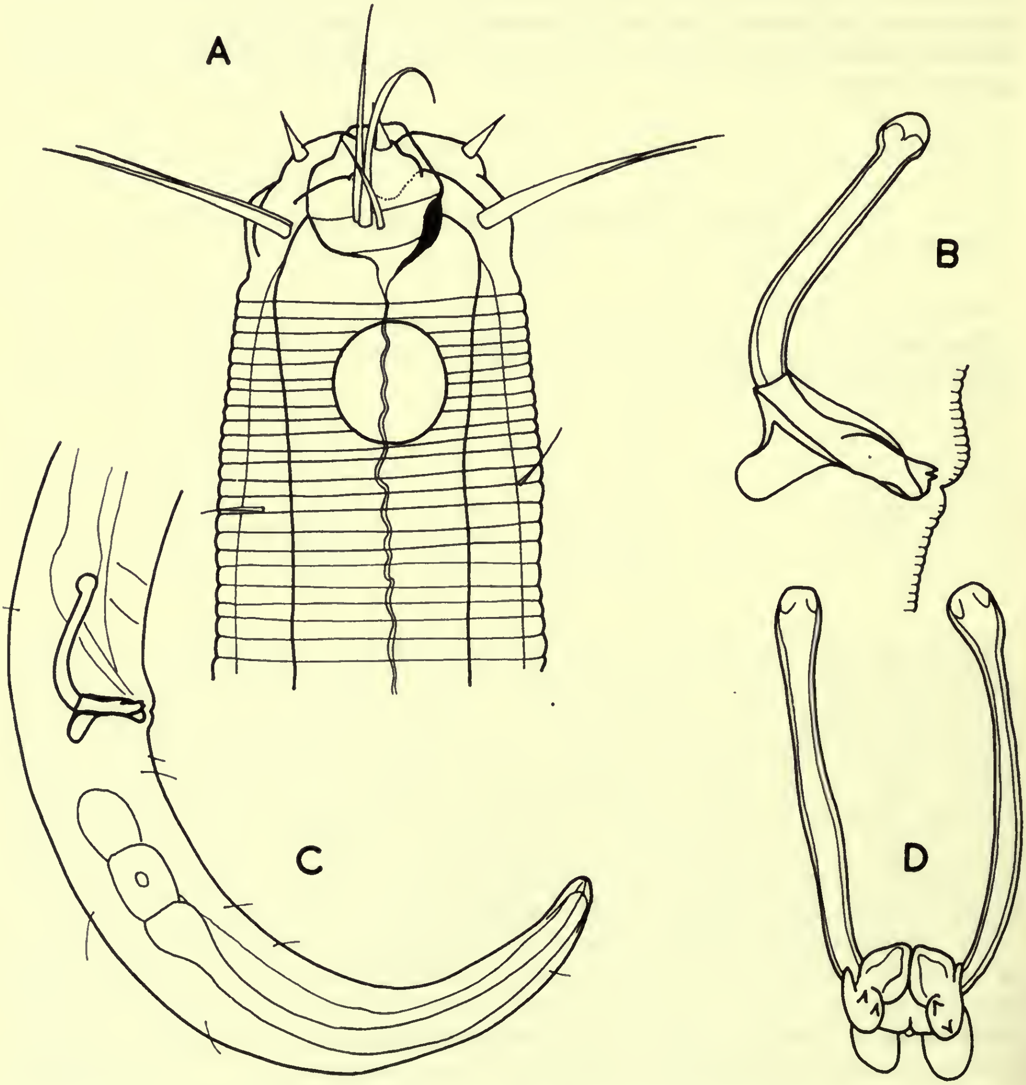


Fig. 10. *Theristus* (*Theristus*) *interstitialis* sp. nov. A, Lateral view of male head. B, Lateral view of spicules and gubernaculum. C, Lateral view of male tail. D, Ventral view of spicules and gubernaculum.

Theristus (Trichotheristus) psammoides sp. nov.

(Fig. 11)

Material studied. Three males and three females. B.M. (N.H.), Reg. No. 1968. 271.

Distribution in Exe Estuary. Shelly Bank : M.T.L., M.L.W.N.T., M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	35·63	4·38	8·70	—	1·14
	36·06	4·58	7·99	—	1·19
	32·29	3·90	8·50	—	1·13
Females	30·00	4·31	8·63	63·04	1·38
	29·74	4·04	7·96	60·18	1·13
	28·72	3·86	10·00	64·29	1·12

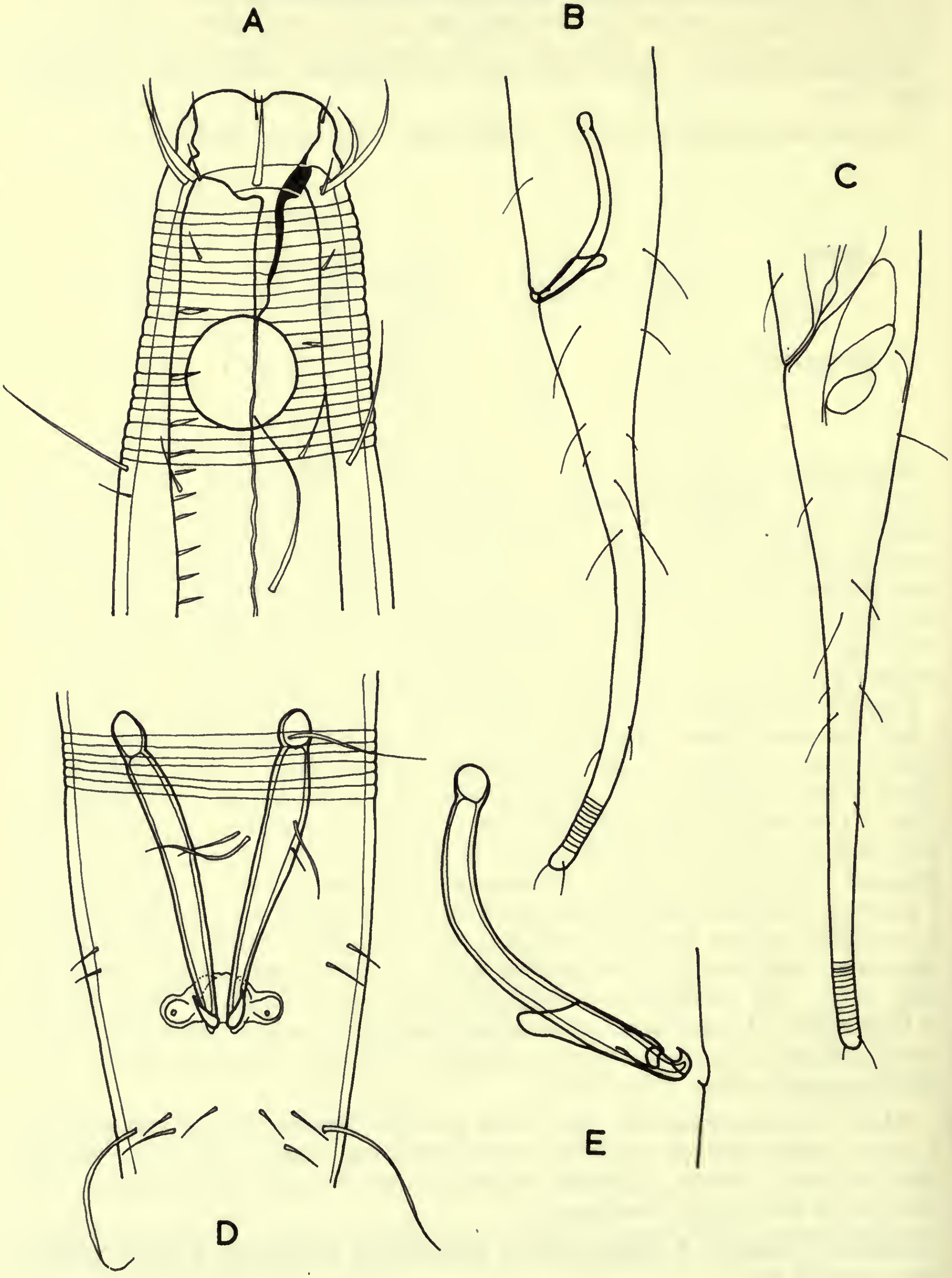
Measurements (in mm. in order of body lengths). Males : Body breadth : 0·032 ; 0·033 ; 0·035. Oesophagus length : 0·26 ; 0·26 ; 0·29. Distance of nerve ring from anterior : 0·104 ; 0·109 ; 0·115. Head diameter : 0·017 ; 0·015 ; 0·016. Length of long cephalic setae : 0·011 ; 0·011 ; 0·012. Amphid diameter : 0·010 ; 0·011 ; 0·012. Body diameter at level of amphids : 0·022 ; 0·021 ; 0·022. Distance of amphids from anterior : 0·018 ; 0·017 ; 0·021. Length of longest body setae : 0·024 ; 0·023 ; 0·029. Tail length : 0·131 ; 0·149 ; 0·133. Cloacal diameter : 0·028 ; 0·028 ; 0·027. Spicule length : 0·041 ; 0·041 ; 0·043. Gubernaculum length : 0·016 ; 0·014 ; 0·017.

Females : Body breadth : 0·046 ; 0·038 ; 0·039. Oesophagus length : 0·32 ; 0·28 ; 0·29. Distance of nerve ring from anterior : 0·126 ; ? ; ?. Head diameter : 0·017 ; 0·016 ; 0·017. Length of long cephalic setae : 0·013 ; 0·013 ; 0·014. Amphid diameter : 0·007 ; 0·008 ; 0·009. Body diameter at level of amphids : 0·025 ; 0·024 ; 0·023. Distance of amphids from anterior : 0·017 ; 0·017 ; 0·020. Length of longest body setae : 0·037 ; 0·036 ; 0·037. Tail length : 0·160 ; 0·142 ; 0·122. Anal diameter : 0·031 ; 0·026 ; 0·029. Distance of vulva from anterior: 0·87 ; 0·68 ; 0·72.

There are six small slender labial setae and ten cephalic setae, of which four are very slightly shorter than the remaining six. In some specimens four additional very short setae (about 4μ) can be detected in association with the submedian pairs (Fig. 11A). The amphids are perfectly circular, and are larger in the males than in the females. Longish setae are scattered generally over the body-surface, but are most numerous in the oesophageal region and on the tail. The tail is filiform for its distal two-thirds (Figs. 11B & 11C).

Male. The gubernaculum has a small rounded dorsally-directed apophysis and a pair of rounded lateral projections at the distal end (Figs. 11D & 11E). The spicules are equal, arcuate, cephalate proximally and strongly hooked distally. The structure of the gonads is not clear.

Female. There is a single anterior outstretched ovary and a small spherical post-vulvular sac.


A
B
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E

DISCUSSION. This species is closest to *T. vicinus* Riemann, 1966, but differs from it in having larger amphids and a different structure of the male copulatory apparatus. It is also close to *T. erectus* Wieser & Hopper, 1967, from which it differs in having larger amphids, no lateral alae and in a differently-shaped gubernaculum.

Family **SPIRINIDAE**

Chromaspirina inglisi sp. nov.

(Fig. 12)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 272.

DISTRIBUTION IN EXE ESTUARY. Orcombe Point : M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	46·00	9·94	20·64	—	1·61
	43·78	10·19	19·52	—	1·62
	48·82	10·00	19·53	—	1·66
Females	38·72	10·34	18·64	58·94	1·51
	46·15	11·11	22.78	62·78	1·80
	42·56	11·09	22·32	63·39	1·83

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·035 ; 0·037 ; 0·034. Oesophagus length : 0·162 ; 0·159 ; 0·166. Distance of nerve ring from anterior : 0·095 ; 0·099 ; 0·097. Head diameter : 0·020 ; 0·014 ; 0·016. Length of shorter cephalic setae : 0·006 ; 0·006 ; 0·006. Length of longer cephalic setae : 0·012 ; 0·011 ; 0·011. Amphid diameter : 0·009 ; 0·010 ; 0·011. Body diameter at level of amphids : 0·023 ; 0·022 ; 0·023. Length of oesophageal bulb : 0·048 ; 0·045 ; 0·043. Breadth of oesophageal bulb : 0·028 ; 0·028 ; 0·026. Tail length : 0·078 ; 0·083 ; 0·085. Cloacal diameter : 0·031 ; 0·033 ; 0·032. Spicule length : 0·048 ; 0·054 ; 0·052. Gubernaculum length : 0·025 ; 0·022 ; 0·023.

Females : Body breadth : 0·039 ; 0·039 ; 0·043. Oesophagus length : 0·146 ; 0·162 ; 0·165. Distance of nerve ring from anterior : 0·082 ; ? ; 0·102. Head diameter : 0·014 ; 0·019 ; 0·020. Length of shorter cephalic setae : 0·005 ; 0·006 ; 0·006. Length of longer cephalic setae : 0·013 ; 0·011 ; 0·012. Amphid diameter : 0·011 ; 0·012 ; 0·010. Body diameter at level of amphids : 0·022 ; 0·026 ; 0·027. Length of oesophageal bulb : 0·043 ; 0·043 ; 0·051. Breadth of oesophageal bulb : 0·028 ; 0·030 ; 0·026. Tail length : 0·081 ; 0·079 ; 0·082. Anal diameter : 0·029 ; 0·028 ; 0·032. Distance of vulva from anterior : 0·89 ; 1·13 ; 1·16. Egg length : 0·123 ; — ; —. Egg breadth : 0·024 ; — ; —.

FIG. 11. *Theristus* (*Trichotheristus*) *psammoides* sp. nov. A, Lateral view of male head. B, Lateral view of male tail. C, Lateral view of female tail. D, Ventral view of male cloacal region. E, Lateral view of spicules and gubernaculum.

The head is invaginated in most specimens. Those with a head diameter of 0·019–0·020 mm. are the least invaginated and this should be taken as the correct head-diameter. The cuticle is marked by fine transverse striations commencing at the anterior border of the amphids and extending to the spinerette on the tail. The body-surface is covered uniformly with very fine hairs, which commence a short distance posterior to the head. These are probably cuticular in origin, but the possibility that they are epigrowths of unicellular cyanophyecous algae cannot be excluded, since these are known to form associations with other species of nematode (e.g.

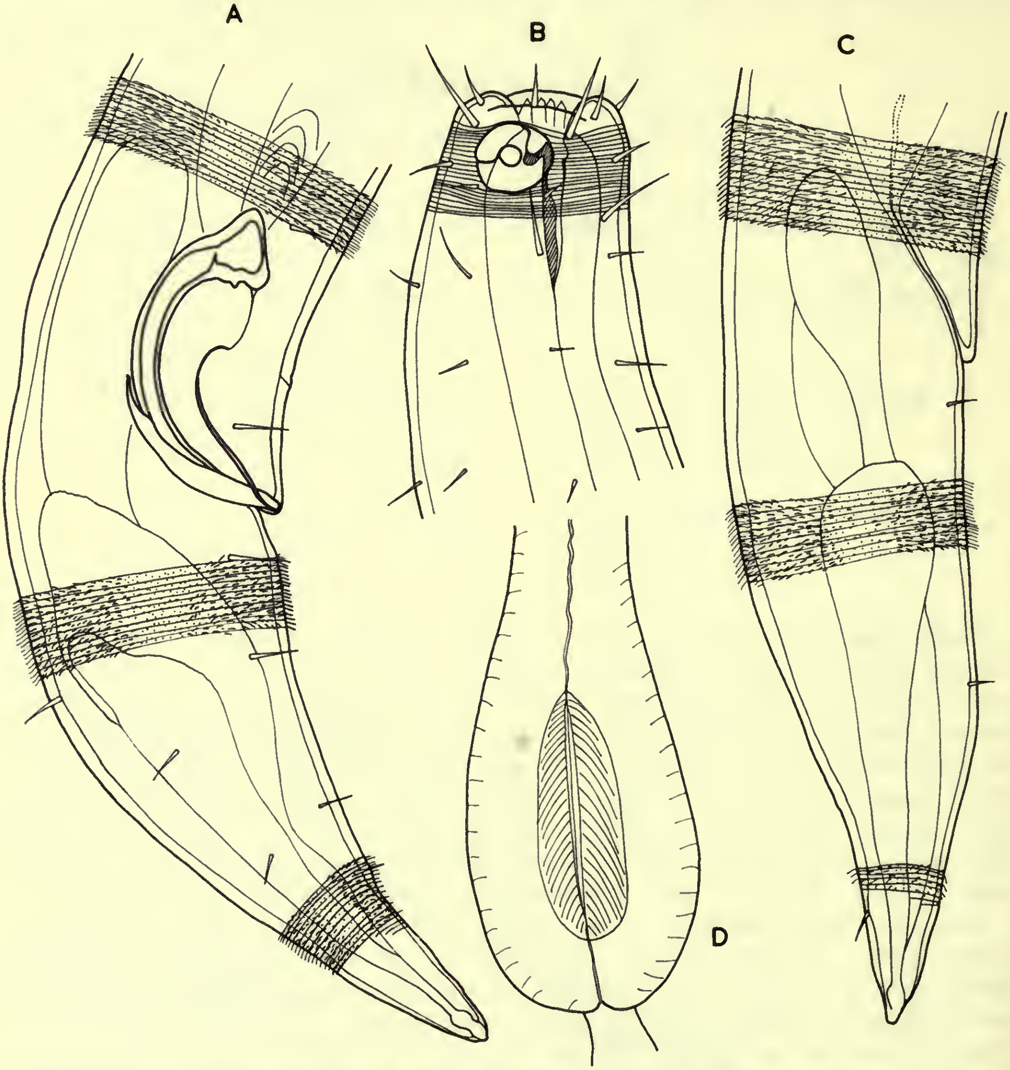


FIG. 12. *Chromaspirina inglisi* sp. nov. A, Lateral view of male tail. B, Lateral view of male head. C, Lateral view of female tail. D, Oesophageal bulb.

Leptonemella species). The lips and labial sense-organs are not visible, because of the invagination of the head. There is an anterior circle of six short cephalic setae, and four longer setae just posterior to them (Fig. 12B). There is a ring of indistinct odontia present in the anterior portion of the buccal cavity, and the posterior portion contains a prominent heavily-cuticularized dorsal tooth opposed by a pair of very small subventral projections. The amphids describe a single rounded loop.

The oesophagus has a pyriform posterior bulb, the cuticular lining of which is not markedly thickened (Fig. 12D). Scattered setae between 0·005 and 0·013 mm. in length extend from the head to about 30% of the way down the oesophagus. The middle region of the body is virtually devoid of setae, but they become fairly numerous on the tail, especially in the male. The tail is conoid, and the spinerette unstriated (Figs. 12A & 12C).

MALE. The gubernaculum is slender and crescentic. It is closely applied to the spicules. The spicules are arcuate, strongly cephalate proximally, and have a prominent ventral ala (Fig. 12A). A small pore is present in the cuticle a short distance in front of the cloaca, but otherwise supplements are absent. The testis appears to be single and outstretched.

FEMALE. The ovaries are paired, symmetrical, opposed and reflexed. The eggs are very elongate.

DISCUSSION. This species is very similar to *C. pontica* Filipjev, 1918, *sensu* Gerlach, 1951, but as Wieser & Hopper (1967) point out the conspecificity of Gerlach's and Filipev's species is doubtful. In the type the amphids are smaller, the cephalic setae only 5μ in length and there are some differences in the structure of the gubernaculum. The present specimens agree with Gerlach's in all respects, except for the uniform covering of fine hairs, which could easily have been overlooked. Otherwise they would appear to belong to the same species.

Family **MICROLAIMIDAE**

Microlaimus spirifer sp. nov.

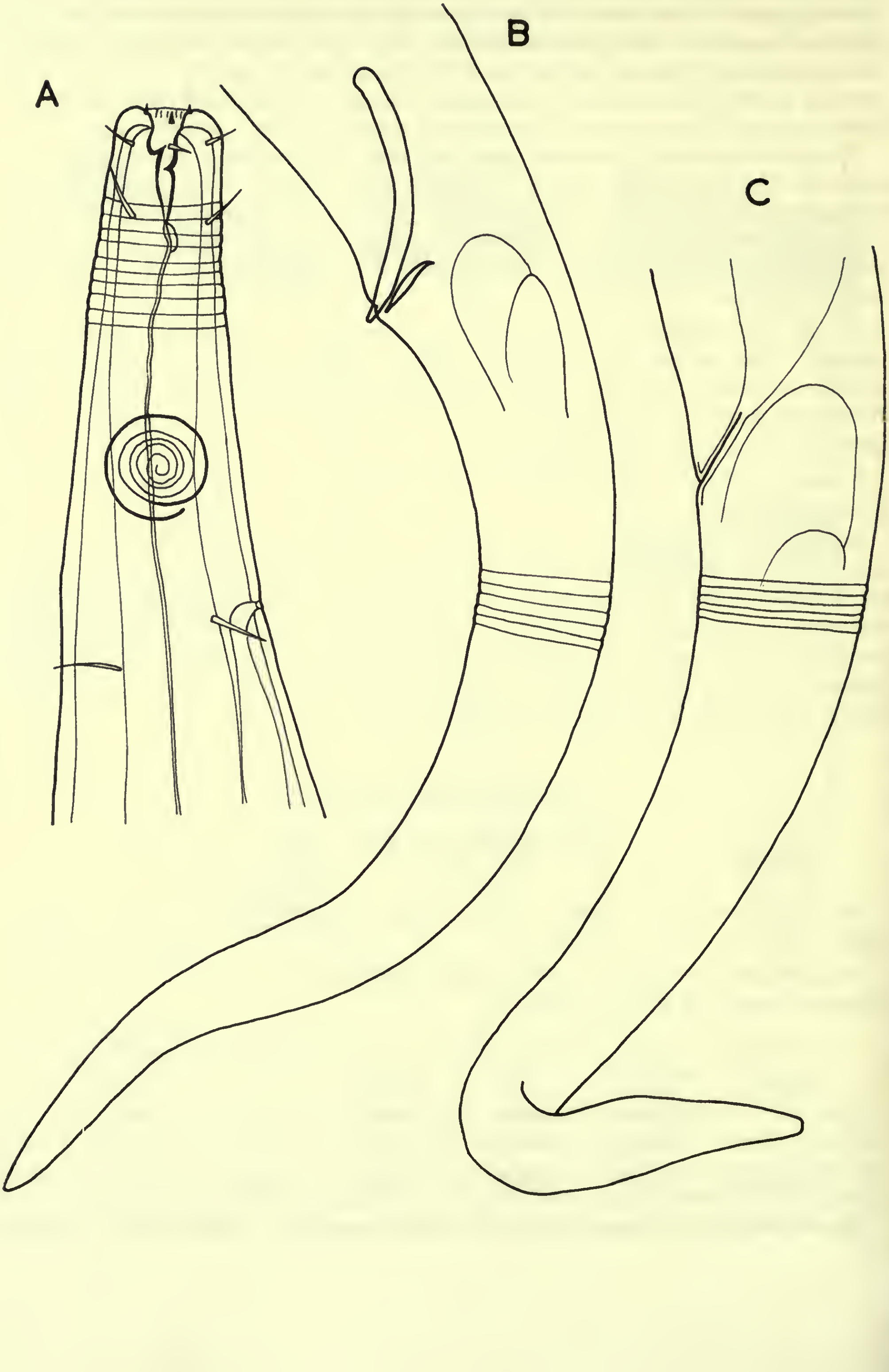
(Fig. 13)

MATERIAL STUDIED. Three males and one female. B.M. (N.H.), Reg. No. 1968. 273.

DISTRIBUTION IN EXE ESTUARY. Shelly Bank : M.T.L., M.L.W.N.T., M.L.W.S.T. Orcombe Point : M.H.W.N.T., M.T.L.

	a	b	c	V%	Body length (mm.)
Males	36·55	7·31	11·16	—	1·06
	38·00	6·69	9·79	—	0·95
	36·67	6·24	8·54	—	0·88
Female	37·67	6·48	9·68	53·26	0·92

MEASUREMENTS (in mm. in order of body lengths). Males: Body breadth :


A
B
C

0·029 ; 0·025 ; 0·024. Oesophagus length : 0·145 ; 0·142 ; 0·141. Distance of nerve ring from anterior : 0·066 ; 0·077 ; 0·087. Distance of excretory pore from anterior : 0·040 ; ? ; ?. Length of oesophageal bulb : 0·032 ; 0·032 ; 0·032. Breadth of oesophageal bulb : 0·021 ; 0·018 ; 0·018. Head diameter : 0·009 ; 0·009 ; 0·008. Length of longer cephalic setae : 0·006 ; 0·005 ; 0·005. Length of shorter cephalic setae : 0·003 ; 0·003 ; 0·003. Length of buccal cavity : 0·010 ; 0·009 ; 0·011. Amphid diameter : 0·009 ; 0·009 ; 0·008. Body diameter at level of amphids : 0·014 ; 0·013 ; 0·012. Distance of amphids from anterior : 0·027 ; 0·024 ; 0·024. Tail length : 0·095 ; 0·097 ; 0·103. Cloacal diameter : 0·017 ; 0·018 ; 0·018. Spicule length : 0·025 ; 0·023 ; 0·022. Gubernaculum length : 0·008 ; 0·007 ; 0·006.

Female : Body breadth : 0·030. Oesophagus length : 0·142. Distance of nerve ring from anterior : 0·083. Length of oesophageal bulb : 0·031. Breadth of oesophageal bulb : 0·020. Head diameter : 0·008. Length of longer cephalic setae : 0·006. Length of shorter cephalic setae : 0·003. Length of buccal cavity : 0·011. Amphid diameter : 0·008. Body diameter at level of amphids : 0·013. Distance of amphids from anterior : 0·024. Tail length : 0·095. Anal diameter : 0·016. Distance of vulva from anterior : 0·49.

The cuticle is transversely striated. The head has the usual arrangement of sense organs ; a ring of six small conical labial papillae, an anterior ring of six short cephalic setae and a posterior ring of four longer setae (Fig. 13A). The buccal cavity is fairly well cuticularized. It contains a dorsal and ventral tooth of about equal size, the dorsal one being the more anterior. There is a very small posterior cavity set off from the main buccal cavity by a constriction. The amphids are spiral, describing about 6·5 turns, the outer margin of the amphid being more prominent than the inner spiral. There are four longish setae situated at about the level of the excretory pore, but otherwise the body is naked. The oesophagus terminates in a pyriform bulb. The tail is long and conoid (Figs. 13B and 13C).

MALE. The gubernaculum is very small, and the spicules are only slightly bent, rounded proximally and pointed distally. There are no supplements.

FEMALE. The ovaries are paired, symmetrical, opposed and reflexed.

DISCUSSION. This species is characterized by the posterior position and spiral form of the amphids, by the form of the copulatory apparatus in the male, and by the long tail.

Family **CYATHOLAIMIDAE**

Pomponema reducta sp. nov.

(Fig. 14)

MATERIAL STUDIED. Three males and three females. B.M. (N.H.), Reg. No. 1968. 274.

FIG. 13. *Microlaimus spirifer* sp. nov. A, Lateral view of male head. B, Lateral view of male tail. C, Lateral view of female tail.

Distribution in Exe Estuary. Shelly Bank : M.L.W.S.T. Orcombe Point : M.H.W.N.T., M.L.W.S.T.

	a	b	c	V%	Body length (mm.)
Males	46·25	7·05	10·96	—	1·48
	43·44	6·18	10·67	—	1·39
	46·25	6·95	9·67	—	1·48
Females	33·33	6·22	10·94	61·79	1·40
	42·65	6·33	10·51	61·38	1·45
	40·79	6·22	10·20	59·35	1·55

Measurements (in mm. in order of body lengths). Males : Body breadth : 0·032 ; 0·032 ; 0·032. Oesophagus length : 0·210 ; 0·225 ; 0·213. Distance of nerve ring from anterior : ? ; 0·093 ; ?. Distance of excretory pore from anterior : 0·117 ; ? ; ?. Head diameter : 0·023 ; 0·022 ; 0·024. Length of labial setae : 0·004 ; 0·004 ; 0·004. Length of cephalic setae : 0·010 ; 0·009 ; 0·010. Amphid diameter : 0·010 ; 0·009 ; 0·010. Body diameter at level of amphids : 0·024 ; 0·024 ; 0·026. Tail length : 0·135 ; 0·138 ; 0·153. Cloacal diameter : 0·030 ; 0·025 ; 0·028. Spicule length : 0·043 ; 0·046 ; 0·046. Gubernaculum length : 0·023 ; 0·026 ; 0·027. Distance of anterior supplement from cloaca : 0·330 ; 0·315 ; 0·295.

Females : Body breadth : 0·042 ; 0·034 ; 0·038. Oesophagus length : 0·225 ; 0·229 ; 0·249. Distance of excretory pore from anterior : ? ; 0·127 ; ?. Head diameter : 0·023 ; 0·024 ; 0·024. Length of labial setae : 0·004 ; 0·004 ; 0·004. Length of cephalic setae : 0·008 ; 0·009 ; 0·010. Amphid diameter : 0·008 ; 0·007 ; 0·007. Body diameter at level of amphids : 0·026 ; 0·025 ; 0·026. Tail length : 0·128 ; 0·138 ; 0·152. Anal diameter : 0·023 ; 0·024 ; 0·025. Distance of vulva from anterior : 0·865 ; 0·89 ; 0·92.

The cuticle is marked by transverse rows of rounded punctuations, and there is a marked lateral differentiation. Punctuations on the head are small, sparse and irregularly arranged, but just posterior to the amphids they become larger and closer together, although still not arranged in definite rows (Figs. 14A & 14B). Along the length of the oesophagus the markings begin to sort themselves into distinct transverse rows, and at the base of the oesophagus the lateral differentiation begins. This comprises four files of larger dots, which gradually increase in size down the length of the body. They are very large and rather irregular in shape in the anal or cloacal region, and extend about two-thirds of the way down the tail-length.

The mouth is surrounded by six small rounded lips each bearing a stout conical labial seta. There are also twelve slender and much shorter setae in positions corresponding with the tips of the buccal rugae (Figs. 14A & 14B). There appear to be only six cephalic setae, each consisting of a stout basal half and a filiform tip. The four shorter cephalic setae reported from all other species of *Pomponema* appear to be absent, unless they are very closely adherent to the larger ones. This reflects the trend begun in *P. stomachor* Wieser, 1954 and *P. polydonta* Murphy, 1963, in which

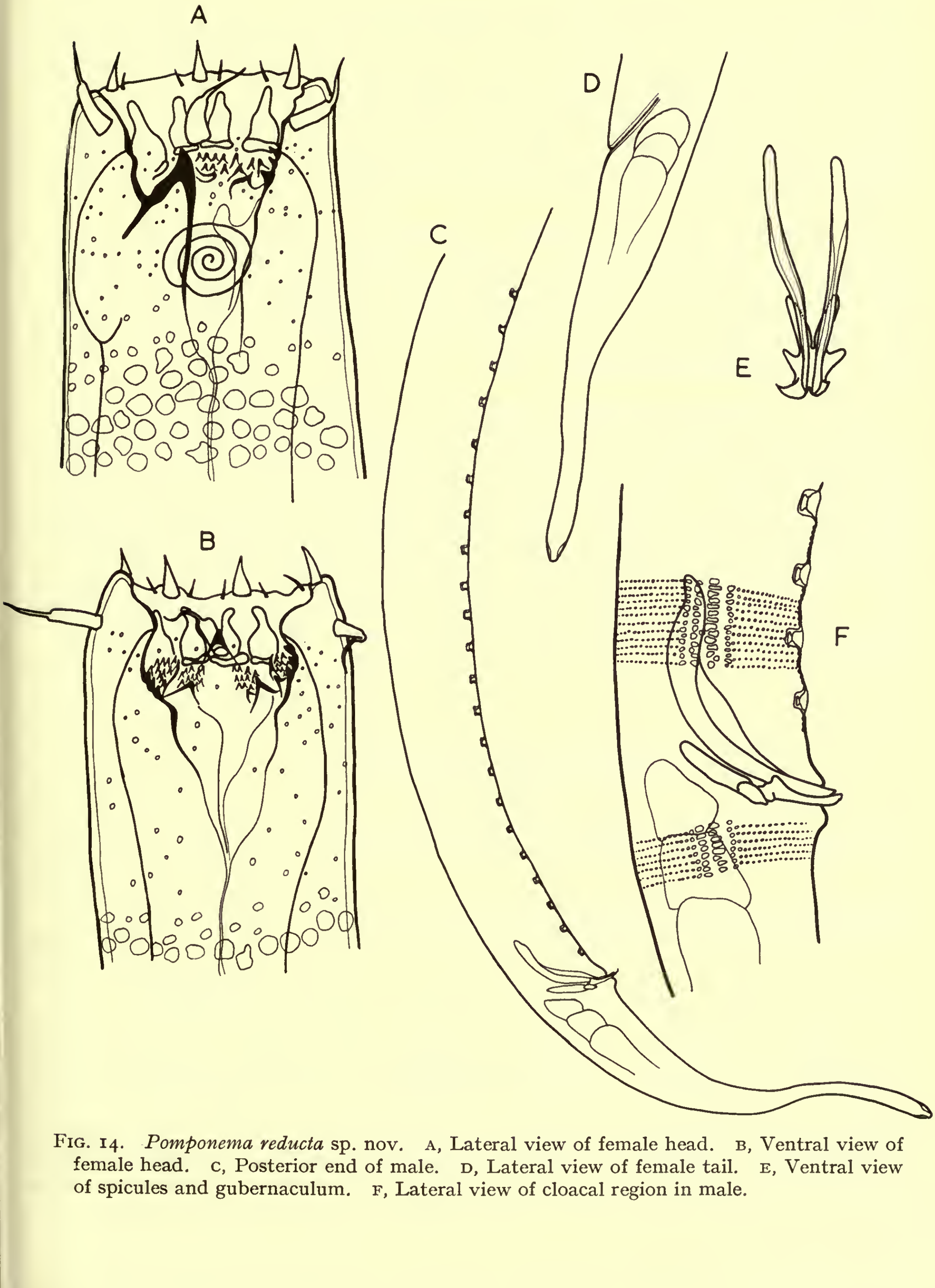


FIG. 14. *Pomponema reducta* sp. nov. A, Lateral view of female head. B, Ventral view of female head. C, Posterior end of male. D, Lateral view of female tail. E, Ventral view of spicules and gubernaculum. F, Lateral view of cloacal region in male.

these four setae are very reduced. The buccal cavity is of the typical form. Anteriorly its walls are supported by twelve buccal rugae. More posteriorly there is a large dorsal tooth opposed by a pair of much smaller subventral teeth and additional groups of denticles arranged as in Figs. 14A and 14B. The amphids describe a spiral of 4–4·5 turns in the male and 3·5 turns in the female.

The oesophagus has a distinct anterior pharyngeal bulb dorsally, and broadens gradually towards its posterior end, with no definite posterior bulb. There are no somatic setae. The tail is long and slender, its proximal half tapering and distal half filiform (Figs. 14C & 14D).

MALE. The gubernaculum consists of two identical halves each having an outwardly-curving point distally and a rounded lateral projection near the middle (Figs. 14E & 14F). The spicules are arcuate and have small ventral alae. There are 20–24 equally spaced pre-cloacal supplements, the cuticle between them being lamellated and giving them the complex appearance which is characteristic of the genus. The testes are not visible.

FEMALE. The ovaries are paired, more or less symmetrical, opposed and reflexed.

DISCUSSION. This species is closest to *P. polydonta* Murphy, 1963, but differs from it in several respects. The absence of the four shorter cephalic setae has already been noted. In *P. polydonta* the longer cephalic setae are 23μ long as compared with 8–10μ in *P. reducta*. These setae are similar in structure, since Murphy states for *P. polydonta* that 'there is indication of segmentation and articulation of larger setae on some specimens at a point one-third to one-half of the length from the base'. The buccal denticles in *P. polydonta* are arranged in two rows, and not in discrete groups as in the present species. The spicules in *P. polydonta* appear to be non-alate.

Paracanthonchus opheliae sp. nov.

(Figs. 15 & 16)

MATERIAL STUDIED. Three males and two females. B.M. (N.H.), Reg. No. 1968. 275.

DISTRIBUTION IN EXE ESTUARY. Shelley Bank : M.T.L., M.L.W.N.T., M.L.W.S.T. Orcombe Point : M.T.L., M.L.W.N.T.

	a	b	c	V%	Body length (mm.)
Males	32·92	9·03	10·09	—	2·14
	37·12	9·13	10·95	—	2·19
	34·33	9·62	10·70	—	2·30
Females	20·65	9·41	12·57	50·00	2·54
	18·46	10·31	11·09	49·62	2·64

MEASUREMENTS (in mm. in order of body lengths). Males : Body breadth : 0·065 ; 0·059 ; 0·067. Oesophagus length : 0·237 ; 0·240 ; 0·239. Distance of nerve ring from anterior : 0·140 ; 0·141 ; 0·137. Distance of excretory pore from anterior : 0·054 ; 0·040 ; ?. Length of longer cephalic setae : 0·018 ; 0·016 ; 0·018. Length of shorter cephalic setae : 0·010 ; 0·009 ; 0·008. Head diameter : 0·031 ; 0·038 ; 0·035. Amphid diameter : 0·014 ; 0·014 ; 0·014. Body diameter at level of amphids : 0·039 ; 0·041 ; 0·040. Tail length : 0·212 ; 0·200 ; 0·215. Cloacal diameter : 0·056 ; 0·055 ; 0·063. Spicule length : 0·059 ; 0·056 ; 0·071. Gubernaculum length : 0·067 ; 0·064 ; 0·065.

Females : Body breadth : 0·123 ; 0·143. Oesophagus length : 0·270 ; 0·256 ; Distance of nerve ring from anterior : 0·177 ; ?. Distance of excretory pore from anterior : 0·052 ; ?. Length of longer cephalic setae : 0·017 ; 0·018. Length of shorter cephalic setae : 0·008 ; 0·010. Head diameter : 0·038 ; 0·053. Amphid diameter : 0·008 ; 0·009. Body diameter at level of amphids : 0·055 ; 0·059. Tail length : 0·202 ; 0·238. Anal diameter : 0·052 ; 0·074. Distance of vulva from anterior : 1·27 ; 1·31.

This is a relatively large species. The cuticle is marked by transverse rows of small rounded punctations which commence at the level of the bases of the cephalic setae. There is no lateral differentiation. Type-1 campaniform organs (see Inglis, 1963) are found in two lateral files down each side of the body, commencing just posterior to the amphids and extending almost to the tip of the tail. In the middle of the body these files are about 16μ apart. There are six files of setae down the length of the body, and these are shorter and more widely spaced posterior to the base of the oesophagus.

In all specimens the head is somewhat invaginated, so that the labial sense-organs cannot be seen. The arrangement of cephalic setae is typical of the genus, with an anterior ring of six short setae and more posteriorly four longer setae. The buccal cavity is cyathiform and contains twelve buccal rugae. The dorsal tooth is relatively small (Fig. 15A). The amphids in the male describe a spiral of 4 turns and in the female 3·5 turns. There are two large ocelli positioned dorsolaterally 1–1·5. head diameters from the anterior. They each consist of an anterior lensatic unit and a posterior chomatic unit containing dark blackish pigment granules. The pigment can only be seen in living or freshly killed specimens, and is removed completely on clearing in glycerine.

The oesophagus is more or less cylindrical throughout its length. Numerous large pennate diatoms were seen in the gut of several specimens. The tail is conical (Figs. 15D & 16) and in the male bears two files of longish ventrolateral setae.

MALE. The spicules are curved and have broad ventral alae. They are pointed distally and the proximal end has an undulating appearance (Figs. 15B & 15C). The gubernaculum is a complex paired structure, the distal end of which is set off from the long proximal portion as a pair of massive swellings which appear rectangular in lateral view. Each swelling bears three large teeth, the arrangement of which is shown in Figs. 15B & 15C. Anteriorly two small protuberances project from the distal portion of the gubernaculum on either side of the spicules. The proximal part of the gubernaculum consists of two long club-shaped structures which lie very

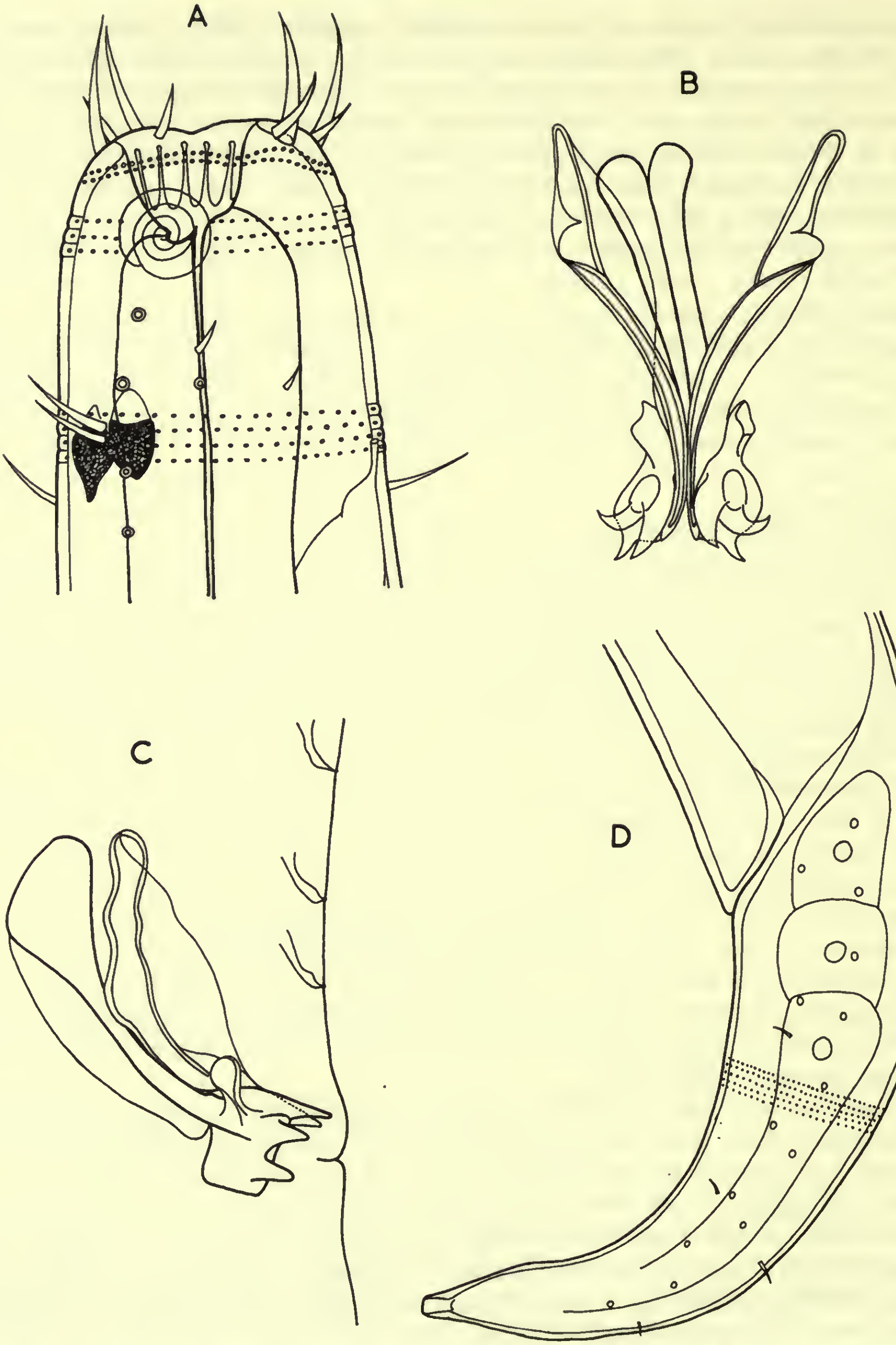


FIG. 15. *Paracanthonchus opheliae* sp. nov. A, Lateral view of male head. B, Ventral view of spicules and gubernaculum. C, Lateral view of spicules and gubernaculum. D, Lateral view of female tail.

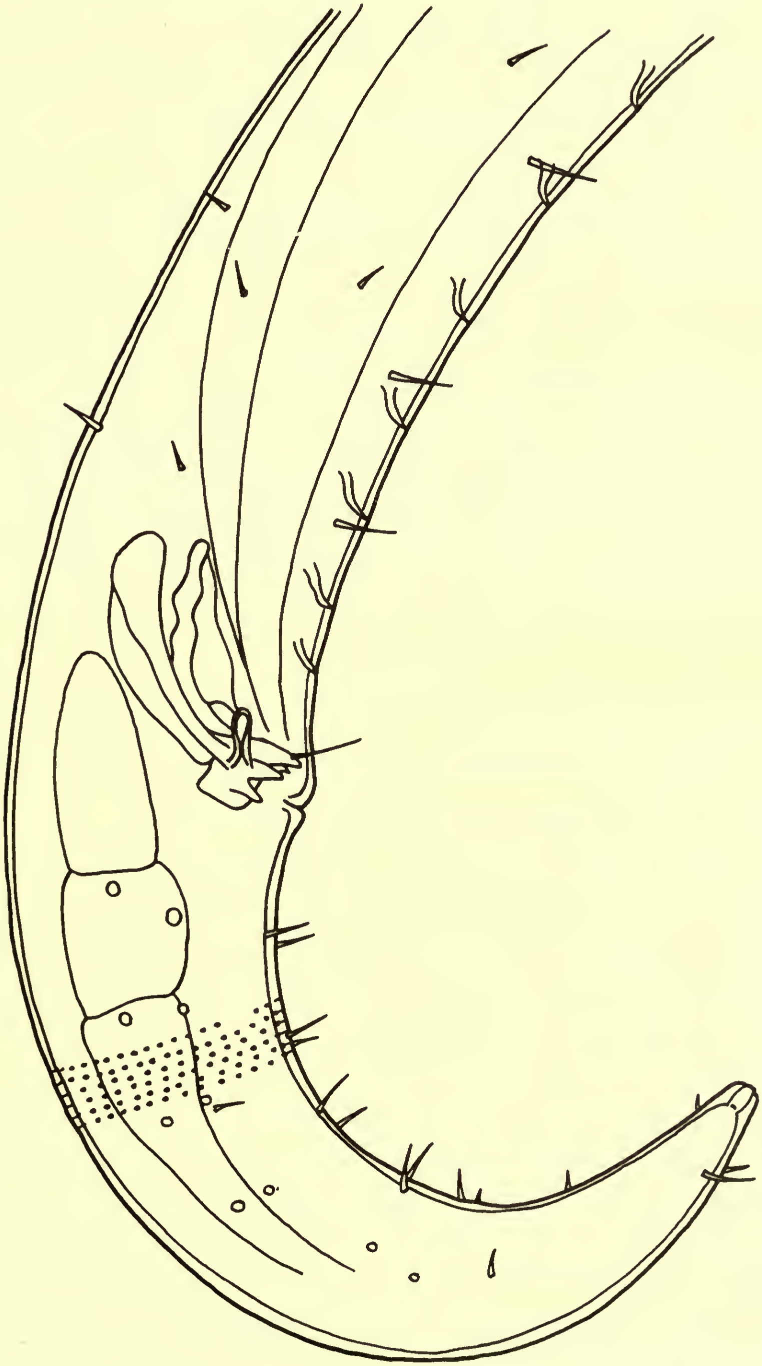


FIG. 16. *Paracanthonchus opheliae* sp. nov., lateral view of male tail.

close to one another. They bear narrow alae along their dorsal edges. There are seven tubular pre-cloacal supplements arranged as in Fig. 16. The testes are paired, opposed and outstretched, the anterior one commencing about one-third of the way down the length of the body.

FEMALE. The ovaries are paired, symmetrical, opposed and reflexed. The eggs are roughly spherical, about 65μ in diameter.

DISCUSSION. This species belongs to group 'B' in the key of Wieser (1954). It differs from all other species assigned to this group in the structure of the gubernaculum and spicules.

ACKNOWLEDGEMENTS

The main part of this work was conducted at the University of Exeter under the supervision of Professor L. A. Harvey, for whose advice and encouragement I am very grateful. I should also like to thank Dr. W. Grant Inglis and Mr. John W. Coles of the British Museum (Natural History) for my initial instruction in nematode taxonomy and for the continued assistance and hospitality they have afforded me on subsequent occasions. I am indebted to Mr. S. Prudhoe for critically reading and correcting the manuscript. The work was supported by a grant from the Natural Environment Research Council.

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THE ANATOMY AND TAXONOMY OF *INDOSTOMUS PARADOXUS* PRASHAD & MUKERJI

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K. E. BANISTER

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BY

KEITH EDWARD BANISTER

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THE ANATOMY AND TAXONOMY OF *INDOSTOMUS PARADOXUS* PRASHAD AND MUKERJI

By K. E. BANISTER

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ABSTRACT

The osteology of *Indostomus paradoxus* Prashad and Mukerji is described and the evidence for its affinities discussed. The array of characters common to both *Indostomus* and the higher paracanthopterygii suggests a relationship between the two groups which is expressed by proposing a new paracanthopterygian order—Indostomiformes—of which the only known representative is *Indostomus paradoxus*.

INTRODUCTION

Indostomus paradoxus was discovered by the Indian Museum Expedition of 1926 in Lake Indawgyi, a large shallow lake in the Myitkyina district of Upper Burma. The series of specimens collected (about 30) was named and briefly described by Prashad and Mukerji (1929). Most of the specimens were housed in the Indian Zoological Survey in Calcutta, except for five which were presented to the British Museum (Natural History) and at least one was presented to the United States National Museum.

Bolin (1936) briefly redescribed the U.S. National Museum specimen but the unavailability of further specimens resulted in the only two descriptions of this species being superficial.

Materials and Methods

One of the five specimens at the B.M. (N.H.) [No. 1937.9.25 : 1–5] had been prepared by the alizarin method but was not suitable for detailed examination. I was, therefore, delighted to receive another specimen from Dr. Earl Herald of the Steinhart Aquarium, California Academy of Sciences (CAS-ACC 1963–xii–16). This fish was one of six which arrived at an aquarium fish importers in America and was described as having come from "Mountain streams remote from Bangkok". Doubt has since been cast on this locality (Herald pers. comm.). I prepared this fish by the alizarin method and dissected it.

Since then I have obtained about 140 specimens from Dr. Alan Tubb of the F.A.O. in Thailand. Dr. Tubb collected them from a stream at the west side of Lake Indawgyi in 1956, kept them alive in Aquaria and made invaluable notes on their behaviour (see Appendix 1). It is with great pleasure that I acknowledge his kindness in making both his notes and specimens available to me.

Some of the specimens have been stained with alizarin and dissected as before. I have also had prepared longitudinal and transverse serial sections, stained in Mallory's triple stain. Other specimens have been presented to various museums throughout the world.

The size range of the specimens was 21–27 mm. (standard length). The line drawings of the bones were made from different specimens but all were within the 24–27 mm. s.l. range.

Terminology

The bone terminology generally follows Harrington (1955) although with only adult specimens available I cannot be too certain about the dual origin of some bones ; in these cases the dermo- and auto-prefixes will not be used. The terms dentary, angular and articular are retained for the three bones of the lower jaw. I fully accept the inaccuracies implied in this but it is a convenient labelling system (Weitzman 1962), especially in the absence of embryological information.

Nelson (1967) has been followed for the naming of the pharyngeal bones.

Greenwood *et alii* (1966) have been followed for classification above the genus level. The names given to the muscles are merely indicative of their position and function ; identity with muscles of the same name in other fishes is not necessarily intended.

THE OSTEOLOGY OF *INDOSTOMUS PARADOXUS*

The body of *Indostomus* is very slender, slightly depressed and covered in scutes (fig. 1). The presence of this dermal armour has had a modifying effect upon the axial skeleton and musculature.

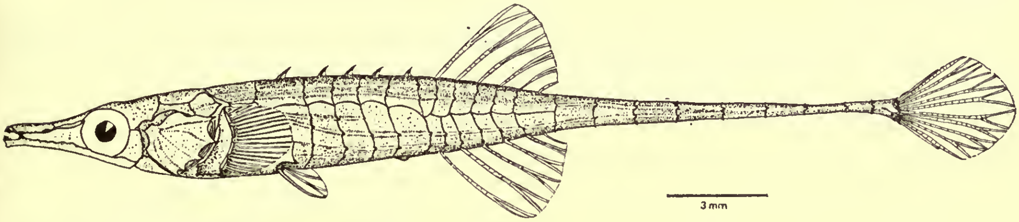

Fig. 1. *Indostomus paradoxus* Prashad and Mukerji. Lateral view.

Body Armour

In the abdominal region there is a median row of dorsal plates and two rows of ventrolateral plates. The latter irregularly overlap in the ventral midline and their dorsal edges overlap the ventral margins of the dorsal plates. In front of the last dorsal fin ray the dorsal plates are convex, behind it they are flat. The plates are also flattened on the ventral surface of the abdomen.

There are twenty-one dorsal plates (rarely twenty) corresponding in number, but not always in position, to the vertebrae. The first plate is loosely connected to the head by a fold of skin which allows the fish to move its head (see Appendix 1). Each of the next five plates (Nos. 2 to 6 inc.) bears at its centre a small mobile spine which supports a flap of tissue. The depression in which each spine articulates is perforated by a pair of tendons attached to the muscles fastened on to the median keel of the plates. The articulation mechanism of one of the spines is shown in fig. 2.

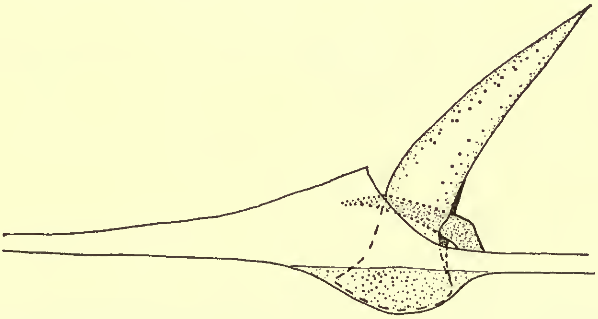

Fig. 2. Diagram of the articulation of one of the dorsal spines.

The first ventrolateral plate has been incorporated into the pectoral fin skeleton (see below). The anteroventral margin of the second has been expanded forwards and lies below the pectoral fin. A notch in its posterior margin marks the position of the articulation of the pelvic fin, which is on the third plate (fig. 1). The first five dorsal and anal fin rays articulate between the plates ; the sixth, like the isolated dorsal spines, is in the centre of the plate. Posterior to the median fins the plates become fused to give the body a quadrangular cross section. A series of cristae run along the length of the body ; towards the caudal region they coalesce and emphasize the rectangular cross section of the caudal region.

Vertebral column

There are 21 (rarely 20) vertebrae, of which nine are abdominal. Transverse processes, which originate at the base of the anterior part of the neural arch, are present on vertebrae 2–9 inclusive (figs. 3 and 4). Ribs are absent.

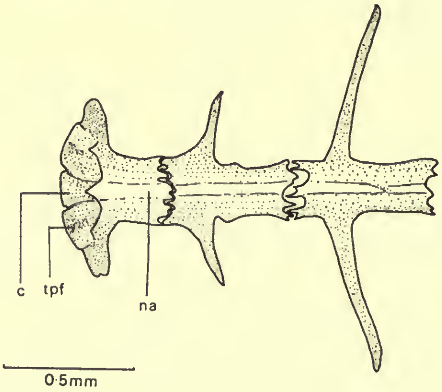

FIG. 3. Dorsal view of the first three vertebrae. For explanation of the abbreviations see key on page 207.

The first vertebra (figs. 3, 4, and 12) is modified to allow for the depression and elevation of the head (see Appendix 1). The transverse processes are broad and arise from the centrum. A part of the leading edge of each transverse process is extended forward as a shallow socket to receive the exoccipital process dorsally (figs. 4 and 12). The neural arch of the first vertebra is fused to the centrum and has a sloping anterior face to permit the elevation of the head. This elevation is effected by the contraction of epaxial muscles which are connected to the epiotics by ossified tendons. I am unable to explain the mechanism which causes the lateral flexures of the head noticed by Dr. Tubb (see Appendix 1).

The transverse processes on the abdominal vertebrae do not contact the dermal plates. The neural arches of the abdominal vertebra (fig. 4) have a complex interdigitation with each other ; neural spines are not formed.

The last abdominal vertebra (the ninth) has short, thin transverse processes and the posterolateral edges of the centrum develop as small wings which articulate with the front edges of the haemal arch of the tenth vertebra. Vertebrae 11–21 (or 20) have neural and haemal arches which become progressively shallower and after the fourteenth vertebra fuse with the dermal armour so that the nature of the neural spine of the last caudal vertebra cannot be determined.

A series of ossified tendons lies horizontally in the axial musculature. Some originate on the ventral keels of the dorsal row of plates, others originate in the musculature, but all run caudally to transmit the contractions of the anterior muscles to the posterior part of the body. A cross section of one segment of the caudal region reveals an external ring of armour divided vertically by the vertebra, with four groups of tendons ; situated above and below the centrum on each side. Very little musculature is present.

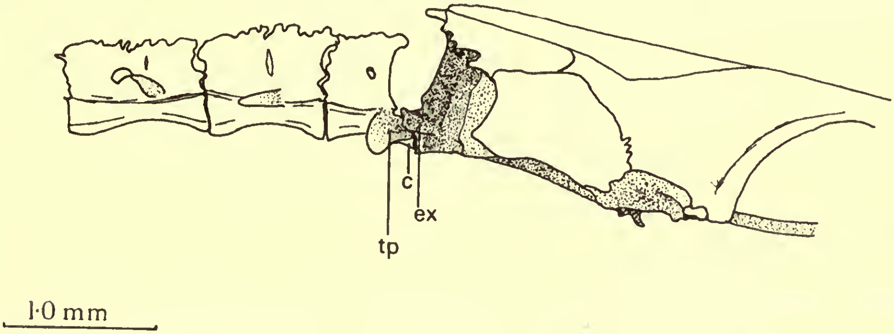

FIG. 4. Lateral view of braincase and anterior vertebrae to show the occipital articulation.

Caudal fin

The caudal fin is large and fan-shaped (fig. 1). It is dorsoventrally symmetrical and in each half there are two small procurrent rays, one principal unbranched ray and four or five branched rays (figs. 1 and 5).

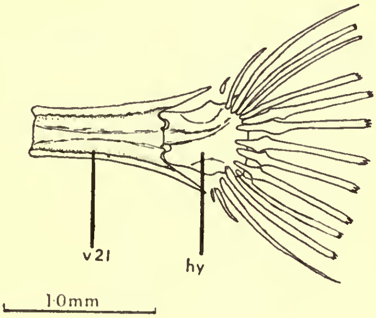

FIG. 5. Caudal fin skeleton.

The caudal skeleton consists of a preural centrum fused with the hypurals into a single solid unit. It is extremely small and no evidence of any fusion of parts is available.

Median fins and their skeletal supports

The isolated dorsal spines which may represent the first dorsal fin have been mentioned above. The median keels of the dorsal plates (fig. 6) appear to fulfil the function of proximal radials for all the median fin rays. The dorsal and anal fins both have six segmented rays, all but the last being branched. Differences in the position of branched and unbranched rays relative to the scutes has been commented on above (and see fig. 1). A small nodule of cartilage (the distal radial?) is found between the bases of the lateral halves of each fin ray.

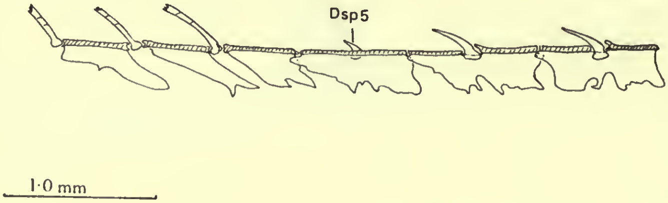

Fig. 6. Diagram of the last three dorsal spines and the first three dorsal fin rays to show the fin supports. The fifth spine is out of alignment.

Pectoral fin skeleton

The pectoral fin has 23 rays, of which 15 are segmented. The supracleithrum (fig. 7) is lodged ventrally in a niche on the first lateral scute which has been incorporated into the pectoral skeleton. Functionally, the cleithrum is represented by this first scute and the median flange on its anterior edge, but it is probable that the flange alone represents the cleithrum which has fused with the scute. The outer part is ornamented in the same way as the other scutes and is clearly in series with them. Only the flange forming the hind wall of the gill chamber really distinguishes it. I hesitate to refer to the scute-like part of this bone as an infracleithrum (Swinnerton 1905) which is a similar bone in *Gasterosteus*, because of the position of the supracleithrum. Applying Occam's razor the most likely explanation is the fusion of the cleithrum and the scute. The cleithra interdigitate in the midventral line.

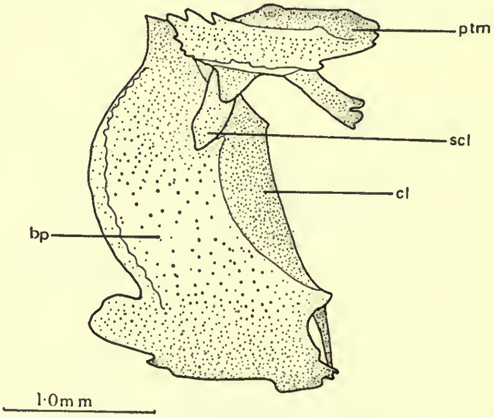

Fig. 7. Lateral view of the dermal elements of the pectoral fin skeleton.

The endochondral part of the pectoral skeleton consists of a coracoid, a scapula and three pterygials (fig. 8). Baudelot's ligament is absent.

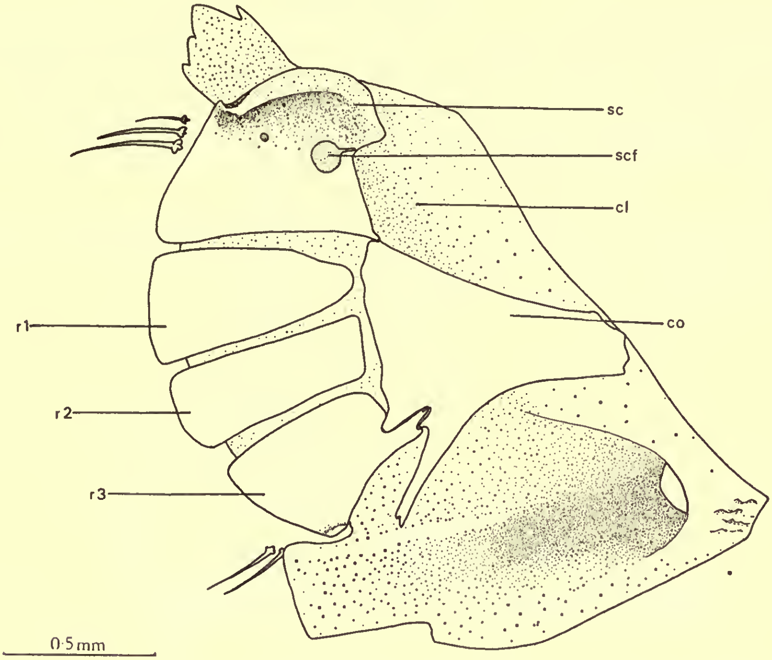

FIG. 8. Medial view of the pectoral fin skeleton. Only the upper and lower pectoral fin rays have been drawn in.

The coracoid has a posteroventral process which rests on the cleithrum. The scapular foramen is contained entirely within the scapula and only just fails to open anteriorly. The dorsal margin of the scapula is expanded horizontally, and laterally it fits closely on to the dorsal edge of the scute. The recess below the dorsal lip of the scapula on its median face houses the origin of muscles which run to the pectoral fin. The coracoid, scapula and pterygial ossifications are all contained within a sheet of cartilage and are joined to each other more firmly than they are to the rest of the pectoral skeleton. There is a possibility that the scapula has fused with the uppermost pectoral pterygial. This has happened in other fishes eg. *Scorpaenichthys* (Starks 1930) and would account for the low number of pterygials.

Pelvic fin and skeleton

The pelvic fin consists of four segmented rays. The outermost ray is thickened, and the middle two branched. The base of the fin articulates on a small boss in the centre of a depression near the rear margin of the second ventrolateral scute (fig. 1). Rays 2, 3 and 4 share either one elongated or two small rounded ossicles lying between their divided bases. The first ray is not so markedly bifurcated at the base and articulates directly with the boss.

The pelvic girdle is reduced to a small ridge of bone in the medial face of the scute.

SYNCRANIUM

The skull is fairly flat on top and rather depressed. The dermal bones are pitted and ridged, with most of their edges crenellated or spiny. A series of ridges on the skull (figs. 9 and 10) suggest the presence of an extensive cephalic lateral line system, but close examination of sections has shown that in all probability the lateral line system is confined to a pair of short tubes between and slightly in front of the orbits (see below).

The eyes are large, the snout moderately elongated and the mouth is small and terminal. The most remarkable feature of the mouth is the great discrepancy between the lengths of the upper and lower jaws (fig. 9).

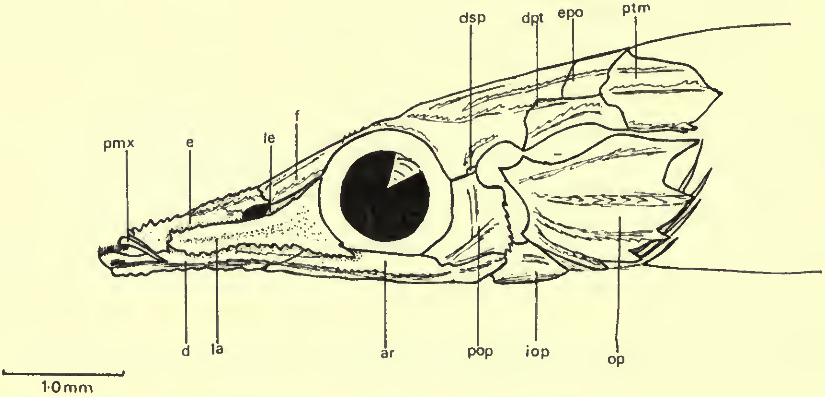

Fig. 9. Head of an unprepared specimen in lateral view. The ridges are illustrated diagramatically.

Olfactory region

The bones present are the ethmoid, lateral ethmoids, supraethmoid and vomer. The nasal bone is absent.

The ethmoid and the supraethmoid are fused together to form one functional unit with the supraethmoid as a dorsal shield over the wedge shaped and largely cartilaginous ethmoid (figs. 10 and 11).

On a few specimens up to four small pits are present near the anterolateral corners of the dorsal surface of the supraethmoid.

The leading edge of the ethmoid block is formed entirely from the supraethmoid and the maxillae and premaxillae are bound to it by fibrous tissue. The anterior nostril (fig. 10 anf) has a flap of skin which directs the water over the olfactory organ and into the canal between the lachrymal and the ethmoid. For most of its length the canal is roofed by the dorsal edges of the supraethmoid and lachrymal which are joined by collagen fibres. The anterior nostril is floored by a process from the ethmoid block which has a ligament joining it to the lachrymal.

The lateral faces of the ethmoid are produced ventrally as sheets for the attachment of the pterygoquadrate arch.

The vomer appears to have fused so firmly with the ventral face of the ethmoid that prolonged maceration will not separate them. Serial transverse sections show that there is no line of weakness nor any sign of a joint between the vomer and the ethmoid. There are two possible explanations for this, but no conclusions can be reached without an examination of much younger fishes than I have been able to obtain. Either there is no vomer, and its place has been occupied by a posterior projection from the ethmoid, or the ethmoid and vomer have co-ossified.

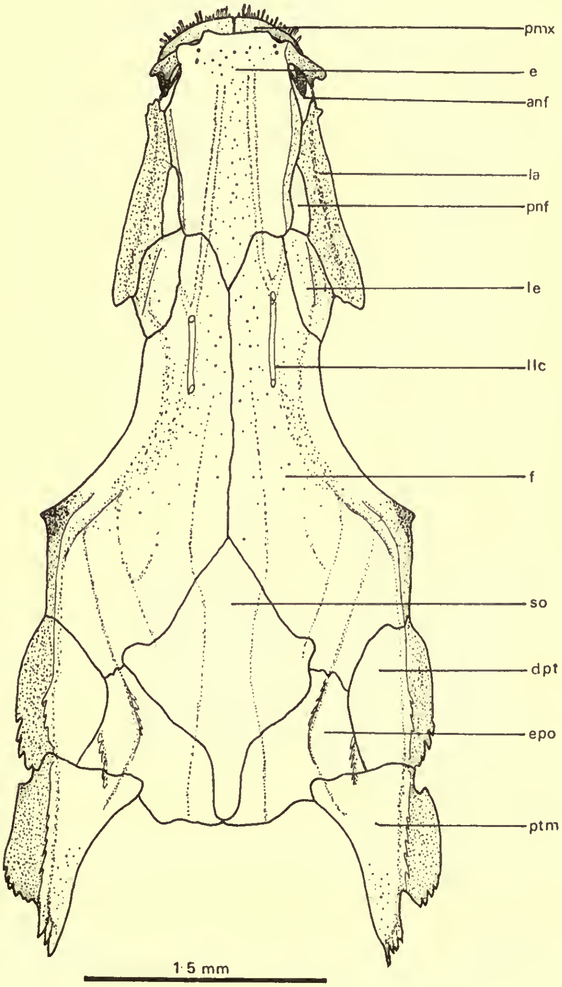

FIG. 10. Dorsal surface of the skull.

For convenience the process in question will be referred to as vomer. It is toothless and has the usual relationships of a vomer bone, except at its anterior end (fig. 11).

The lateral ethmoid (figs. 9, 10, 11) forms the hind margin of the posterior nostril.

Little of this bone is visible in lateral view (fig. 9). The ventral face is concave with the median wall more or less contiguous with the expanded lateral edge of the ethmoid bone. The parasphenoid separates the lateral ethmoids in the midline. The portion of this bone which is visible externally is sculptured, so presumably a prefrontal bone is present as well.

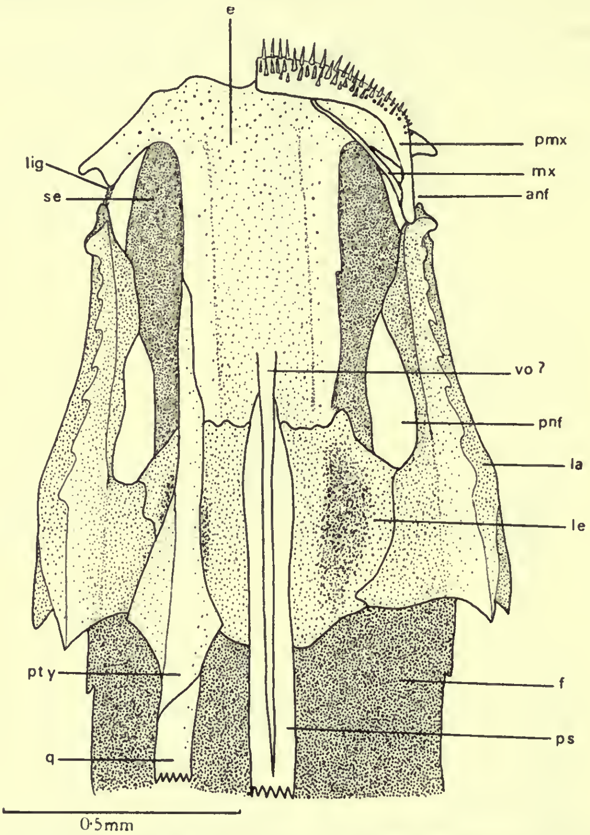

FIG. 11. Ventral surface of the snout. The left pterygoid bar and the right maxilla and premaxilla have been removed.

Orbital Region

The small tubes containing the lateral line canals in the frontals vary in length in different specimens. This is an indication that the cephalic lateral line system has undergone reduction. Small descending frontal processes are present (fig. 12) which form a groove with the lateral, post-orbital part of the frontal. This groove is blocked posteriorly by the sphenotic, and houses what appears to be a part of the muscle block associated with the operculum, although I hesitate to refer to them as dilatator operculi muscles as they are highly modified and also seem to insert on to the preoperculum. The frontals meet in the midline by a series of irregular overlaps.

The pterosphenoids are axehead-shaped bones which just meet each other in the ventral midline above the parasphenoid (fig. 12). The posterior edge of each bone contributes to the margin of the anterior foramen of the pars jugularis of the trigemino-facialis chamber.

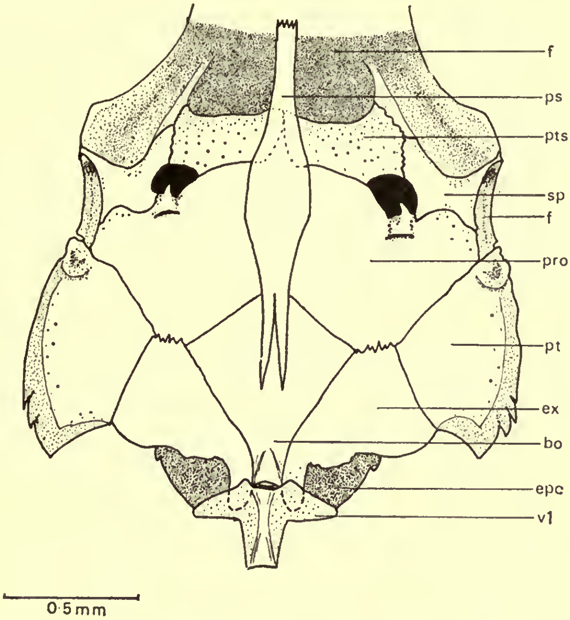

FIG. 12. Ventral surface of the braincase and first vertebra.

The sphenotic is a bone of complex shape, the main part of which resembles a convex cap forming the anteroventral corner of the neurocranium. It forms the lateral margin of the anterior trigemino-facialis foramen (fig. 12). A thin, laterally directed process is present which appears on the external surface of the skull, with the frontal, just behind the orbit (figs. 9, 12). The extremity of this process is expanded and sculptured and may well represent a dermosphenotic. It has been labelled as such in fig. 9.

The parasphenoid penetrates deeply into the cartilage of the ethmoid, and is held in place anteriorly by collagen fibres. Ascending processes are absent and the bone is slightly flattened between the eyes. A thin sheet of muscles originates on the orbital part of the parasphenoid and inserts on the " pterygoid ", this seems to be the adductor arcus palatini.

Only one infraorbital bone is present and that is the lachrymal (figs. 9, 10, 11). The anterior extremity of the lachrymal is joined by a ligament to the ethmoid. The lachrymal forms the outer wall of the olfactory cavity. An examination of the olfactory region reveals the presence of a few strands of tissue which Dr. L. Bannister of Guys Hospital has suggested may well be the remains of a plunger mechanism. The preservation of the fishes is unfortunately not good enough to comment further on this. The plunger (if that is what is it) lies behind the nasal epithelium close to the anterior nostril.

Otic and Occipital Regions

Each prootic is separated from its partner in the midline by the parasphenoid (fig. 12). The distal wall of the trigemino-facialis chamber is thickened and produced anteriorly as a small spike below the anterior foramen for the chamber. From this projection collagenous fibres insert on to the inner face of the hyomandibular. The trigemino-facialis chamber is reduced, the medial wall is missing and only two external foramina are present (fig. 12).

The bone labelled epiotic in fig. 10 appears to have a dermal component which may represent a parietal ossification which has fused with the epiotic. The posterior edge is smooth and is overlain by the first dorsal scute. Two pairs of ossified tendons from the axial muscles insert on this region (see above). A shallow post-temporal fossa is present, floored by the epiotic and pterotic.

Both the dermal and the endochondral parts of the pterotic are present. They can be described as two flat plates meeting at an angle at the lateral edge of the skull with the dermal plate overhanging the endochondral plate (fig. 12). At the widely separated medial edges of the plates, two vertical struts of endochondral bone create a chamber which has three openings. The posterior foramen opens into a cavity on the inner surface of the prootic and the small anterior foramen opens close to the hyomandibular socket. This cavity must largely house the inner ear but there is no trace of otoliths in either whole specimens or in the sections.

The ventromedial corner of the exoccipital is produced backwards, slightly beyond and level with the midpoint of the basioccipital condyle to articulate with the modified transverse processes of the first vertebra (figs. 3, 4, 12). A small pit is present on the posterior wall of the bone in which the descending process of the post-temporal lodges. The foramen magnum is tube-like, and formed mostly from the exoccipitals which just meet dorsally below the supraoccipital. The latter bone has a sculptured surface; there is no occipital crest, just a flat plate narrowly separating the epiotics (fig. 10).

The basioccipital has a convex condyle which does not protrude as far as the exoccipital condyles.

The posttemporal overlies the rear margins of the epiotic and pterotic. The serrated, sculptured dorsal plate is slightly convex (figs. 7 and 10) and from the underside of this there are two processes. The larger central process (fig. 7) abuts onto the exoccipital and the small process has the supracleithrum adhering to its medial face. The supracleithrum does not extend above the cleithrum.

Oromandibular region

The premaxillae are expanded at the symphysis and bear about four rows of fine pointed teeth (fig. 11). The symphysis is weak, the usual jaw ligaments are missing and the upper jaw bones are contained within the fibrous tissue of the upper "lip". Ascending processes are absent (fig. 10).

The maxilla is a greatly reduced, weak bone (fig. 11). Its posterior end is expanded slightly and it is very firmly attached to the dorsal edge of the premaxilla. The length of the maxilla varies from specimen to specimen, in some it almost reaches to the midline. A discussion of the jaw mechanism will be found below. (page 196).

The angular is a small bone, more easily seen in sections than in gross dissection, which lies in a deep pit on the posterior margin of the articular (fig. 13). The articular is greatly elongated and occupies over three quarters of the length of the lower jaw (fig. 13). The lateral face is sculptured and a ridge marking the position of Meckel's cartilage is visible. The tendon from the adductor mandibulae muscles inserts onto the dorsal margin in a gutter formed by the development of a medial shelf below the eye. The anterior end of Meckel's cartilage is medially grooved and receives the posterior projection of the dentary.

A small coronoid process is present near the posterior end of the dentary (fig. 13). The symphysial region is expanded as a dentigerous plate which extends in front of the premaxillary tooth plate so that occlusion only occurs on the posterior half of the former plate.

The seamoid articular is a small, roughly cylindrical bone (fig. 13) in close proximity to the ectosteal part of the articular. It lies in the tendon at the ventral end of the adductor mandibulae muscles which are in an unusual position as a result of the elongation of the mandible (see below).

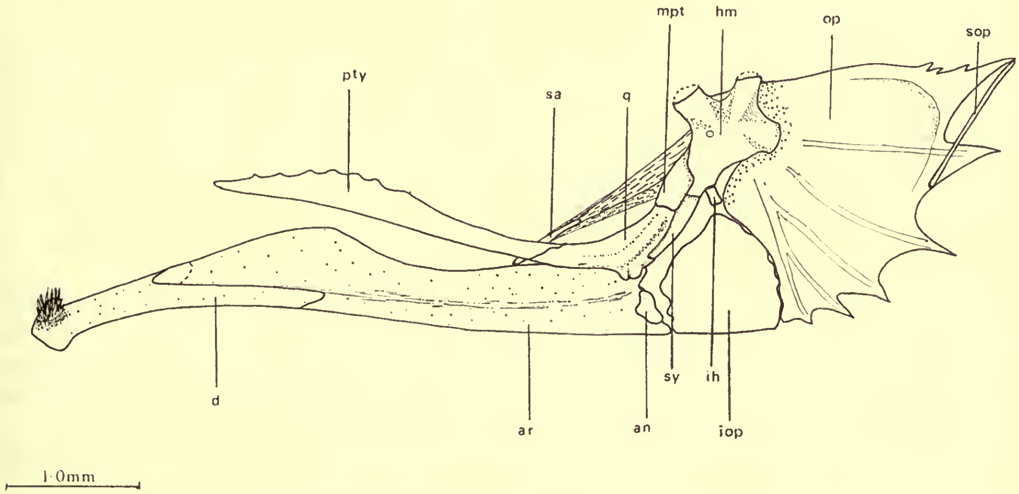

FIG. 13. Medial aspect of the suspensorium, opercular bones and mandible. Part of the medial adductor muscle has been removed to show the sesamoid articular.

Palatoquadrate arch

The palatoquadrate arch lacks the usual complement of bones (fig. 13). One long bone, the " pterygoid ", fills the places usually occupied by the ectopterygoid, endopterygoid and palatine. There is no indication of separate centres of ossification in the adult fish so the real identity of the bone must remain hidden until young stages can be found. In *Gasterosteus* there is a large tri-radiate " pterygoid " bone formed by the fusion of the ectopterygoid and endopterygoid. In the syngnathids the endopterygoid is the largest element whilst in the triacanthid fishes neither the ectopterygoid nor endopterygoid is greatly enlarged. Therefore, just because jaw or snout elongation has occurred, it cannot be stated that certain pterygoid elements necessarily enlarge, fuse or disappear.

If the vomer has co-ossified with the ethmoid block (see page 189) then there are slight grounds for offering the suggestion that the descending sheets on the ventral face of the ethmoid represent anterior suspensorial bones (probably the autopalatines) fused with the ethmoid as an added strengthening member. This must remain conjectural however until the ontogeny is known.

The " pterygoid " is largely a thin lath of bone with the dorsal margin below the eye bent over laterally to conform to the curvature of, and to support, the eye. In front of this, a dorsal lamella develops at an angle to the rest of the bone to form the groove which will anteriorly hold the descending sheets from the ethmoid (fig. 11). At the widest part of the pterygoid, just at the front of the orbit, a ligament joins it to the lachrymal.

The quadrate has an elongated lower limb (fig. 13), with the articular condyle as a transverse cylinder placed ventromedially—dorsolaterally at its heel. The dorsal limb is shorter than the ventral limb but extends further on the medial side where it overlaps the metapterygoid. The posterior edge of the quadrate is channelled to receive the symplectic.

The metapterygoid dorsally articulates with the hyomandibular, and the ventral part of its posterior margin contacts the symplectic. Both the metapterygoid and the dorsal blade of the quadrate are angled more towards the midline than is the rest of the suspensorium. The symplectic is a thin conical bone which is housed in a groove on the rear edge of the quadrate (fig. 13). It is poorly ossified and has a synchondrosis with the hyomandibular.

Opercular series

The operculum is armed with six conspicuous spines (fig. 13). The hyomandibular socket faces forwards at the anterodorsal edge of the bone. Medially, the posterior margin bears a shelf underneath which the levator operculi muscles from the hyomandibular insert. The dilatator operculi muscles insert on the anterior projection of the operculum in front of the hyomandibular socket.

The suboperculum is greatly reduced to a thin rod inside the posterior margin of the operculum (fig. 13).

The interoperculum is a flat sculptured bone connected to the mandible by a short but ill-defined interoperculo-mandibulare ligament. A loose interdigitation exists between the interoperculum and the operculum.

The preoperculum has a firm ligamentous connection to the quadrate along its ventral edge. The greatest expansion of the adductor mandibulae muscles occurs in the space between the preoperculum and the suspensorium.

Hyoid arch

The interhyal is a flat quadrangular bone with its dorsal margin fitting into a transverse groove in the posterior face of the hyomandibular (fig. 13).

The epihyal and ceratohyal are ankylosed dorsally and both have a depressed section (fig. 14). There is no foramen in the ceratohyal. Two slender branchiostegal rays articulate on the lateral face of the slender part of the ceratohyal and two

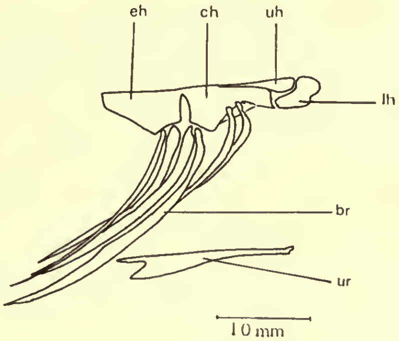
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FIG. 14. Lateral aspect of the hyoid bar, branchiostegal rays and urohyal.

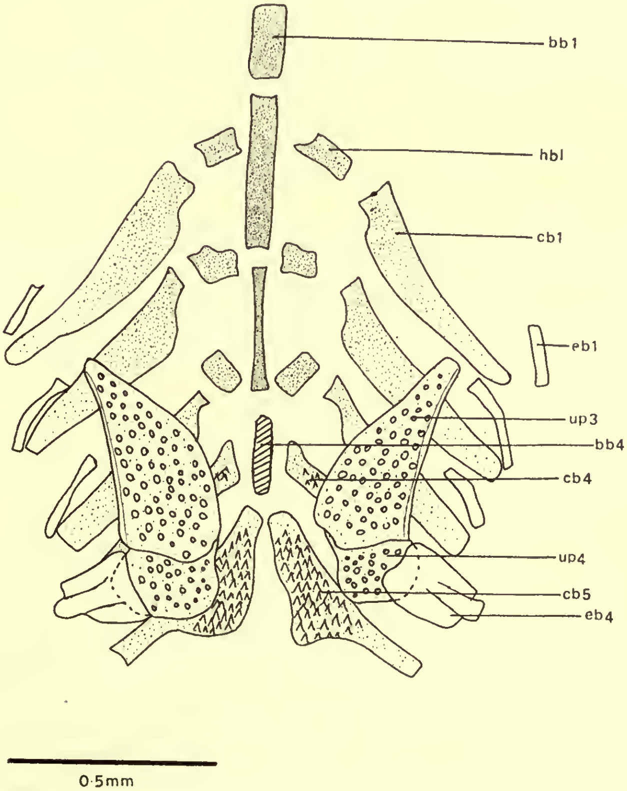
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FIG. 15. Dorsal view of the pharyngeal skeleton. Basibranchial 4 is cartilaginous.

thicker rays articulate on the same face of the expanded part. One thick and one thin branchiostegal ray articulate on the epihyal (fig. 14).

The upper hypohyal is a splint-like bone lying along the dorsal face of the ceratohyal to meet the lower hypohyal (fig. 14).

The basihyal is a flat bone about four times as long as it is wide. The urohyal (fig. 14) is keeled and the posterior half of the bone is protected ventrally by a triangular median dermal plate which lies in front of the first ventrolateral body plates.

The hyomandibular (fig. 13) is a roughly cuboidal bone with the foramen for the hyomandibular nerve below the anterior articular head. The sockets on the neurocranium for the hyomandibular are shown in fig. 12.

Branchial skeleton

Ceratobranchials 4 and 5 have fused with tooth plates. Those on the fifth cerabranchials are the larger but they do not meet in the mid-line (fig. 15).

The fourth epibranchial is expanded and lies above the fourth upper pharygeal tooth plate. The larger anterior pharyngeal tooth plate is probably the result of the fusion of the second and third toothplates with the second and third infrapharyngobranchials, the latter being represented by a thickening of poorly ossified endochondral bone along the lateral edge of the plate. There is no trace of the fourth infrapharyngobranchial.

There are three irregularly cuboidal hypobranchials. The fourth basibranchial is distinct but does not ossify.

NOTES ON THE SOFT ANATOMY

1. The jaw mechanism of *Indostomus*

The upper jaw cannot be protruded, the maxillae and premaxillae are bound to each other and to the front of the ethmoid by fibrous tissue. Discrete jaw ligaments are lacking. When the lower jaw is depressed the premaxillae and maxillae rotate about the front of the ethmoid until the distal arm of the premaxilla is vertical. This only allows the jaws to open to a little over 20°. The feeding habits have become modified and are described in the appendix.

The adductor muscles to the lower jaw are small, and are shown diagramatically in fig. 13. They comprise a lateral and a medial muscle. At their insertion they are approximately equal in cross sectional area but before the posterior end of the sesamoid articular the medial muscle has greatly increased in thickness and effectively surrounds that bone. Still further back a band of muscles from the quadrate to apparently the anterior of the operculum separates the medial and lateral adductor muscles. The lateral adductor muscle originates on the hyomandibular. Just anterior to the point of separation of the medial and lateral components the thick medial muscles split into a dorsal and a ventral portion. The dorsal portion originates on the braincase and the ventral portion on the hyomandibular and possibly on the metapterygoid.

I am not certain of the identity of these muscles, and the terms applied to them are used purely descriptively.

2. Swimbladder

The swimbladder is simple and physoclistous. A gas gland and an oval are present.

DISCUSSION

The systematic position of *Indostomus paradoxus*

Indostomus is a bizarre, highly modified fish. Two major factors have combined to obscure its relationships; firstly the great elongation of the lower jaw and secondly the presence of dermal body armour.

The fish fauna of Lake Indawgyi has been listed by Prashad and Mukerji (1929) and does not contain any obvious relatives of this endemic species, so its peculiarities may be due to long isolation in the one lake basin. Prashad and Mukerji put forward the suggestion that the ancestors of *Indostomus* were not fresh water fishes, for in the early Tertiary the Bay of Bengal extended as far as Lake Indawgyi, and some marine fish could have been isolated and confined to the lake when the sea receded, this seems to be the most likely suggestion.

Prashad and Mukerji thought that *Indostomus* was " closely allied to the family Solenostomidae and to a certain extent the Syngnathidae of the order Solenichthyes Regan ". However they pointed out that there were certain differences between the three families. The structures described in this paper show that *Indostomus* is distant from the Syngnathidae and the Solenostomidae. The anatomy of the families comprising the order Gasterosteiformes (*senu.* Greenwood *et alii* 1966) will be described in subsequent papers, but for the moment Jungersen (1910) gives a good account.

Many of the similarities between *Indostomus* and the syngnathids are superficial and due to the presence of the annular armour and an elongated snout. The Syngnathidae and the Solenostomidae both show the following features of taxonomic significance which are not possessed by *Indostomus*.

1. Enlargement and/or complex articulation of the anterior 3 or 4 vertebrae with each other.
2. Sutural contact between the basioccipital and the autopterotic.
3. Separate ecto- and endopterygoids.
4. A metapterygoid which does not ossify as a separate bone but forms the metapterygoid process at the anterodorsal corner of the quadrate.
5. A dorsal lamina on the symplectic.
6. 4 pectoral pterygials.
7. No more than 3 branchiostegal rays.

These characters are enough to suggest that *Indostomus* and the syngnathids are not closely related, or at least should not be placed in the same order.

Bolin (1936) thought that *Indostomus* was closer to the Aulorhynchidae and the Aulostomidae than to the Syngnathidae and Solenostomidae. I hope to show in subsequent papers that the Aulostomidae are closely related to the Syngnathidae and Solenostomidae whilst the Aulorhynchidae is a family of moderately generalized fishes from which the Gasterosteidae are specialized descendants.

The Aulorhynchidae is the most primitive family of the suborder gasterosteoidei in which Greenwood *et alii* (1966) have placed *Indostomus*. Although *Aulorhynchus* and *Gasterosteus* have several features in common and are clearly related there are several reasons why *Aulorhynchus* and *Indostomus* are most unlikely to be related. The trends in the aulorhynchid—gasterosteid lineage have not developed in a direction likely to produce indostomid facies.

Bolin (1936) admitted that the similarities he saw between *Indostomus* and *Aulorhynchus* were superficial, and this is so, but there is one surprising feature that they both possess and that is an elongated mandible. It is relatively much shorter in *Aulorhynchus* than in *Indostomus* but even so it is produced backwards relative to the upper jaw further than in most fishes.

Certain other fishes eg. *Exocoetus volitans* (*Halocypselus* of Gregory fig. 101), *Parachaenichthys* (Chaenichthyidae), Gregory 1933) show the same phenomenon so perhaps one should not place too much weight on this character.

Indostomus and *Aulorhynchus* have few features in common, but because the former is more specialized than the latter many characters of the more primitive fish could have given rise to characters of the more specialized fish. But none of the important features peculiar to *Aulorhynchus* and the gasterosteids are found in *Indostomus*.

Aulorhynchus in particular and the gasterosteids generally have the following characters not possessed by *Indostomus*.

1. Ascending processes on the premaxillae
2. Nasal bones
3. A well formed vomer bone
4. A triradiate " pterygoid " bone
5. Autopalatines
6. An infraorbital series of 5 bones in *Aulorhynchus*, 3 in the gasterosteids
7. Ascending processes on the parasphenoid which contact the frontals
8. An intercalar bone
9. Parietal bones
10. Upper pharyngeal teeth plates consisting of a UP2 and a fused UP3 & 4. In *Indostomus* the anterior element is the larger and may be a fused UP2 & 3, with a separate UP4
11. 4 pectoral pterygials
12. Ribs
13. Pelvic fin skeleton
14. Dermal scutes along the lateral line, not full armour
15. Over thirty vertebrae.

Although many of these differences are only to be expected when comparing a generalized fish with a specialized fish some have been retained by the specialized descendants of aulorhynchids and are not present in *Indostomus*.

Indostomus must therefore be removed from the order Gasterosteiformes as it now stands (Greenwood *et alii* 1966, p. 398). The status of the remaining families in that order will be discussed in subsequent papers.

The next problem is to try and decide which of the higher taxa of Rosen and

Patterson's (1969) modification of Greenwood *et alii* (1966) can best accommodate *Indostomus*. Only the superorders Acanthopterygii and Paracanthopterygii need be considered.

Rosen and Patterson (1969) have included the Atherinomorpha of Greenwood *et alii* (1966) as a series within the Acanthopterygii parallel to the berycoid—percoid lineage. There are certain features of the Atheriniformes which are shared to various extents with *Indostomus*. This does not necessarily imply that *Indostomus* ought to be placed in this order, but rather than it is of a similar level of complexity. This is almost stating the obvious for Rosen (1964) concluded that the Atherinomorpha arose from a group that stood somewhere in the ancestry of the Perciformes, and it is in this zone above the Protacanthopterygii and below the Perciformes that *Indostomus* must lie. The upper limit is set by Gosline (1966) who states that no percoid fish nor percoid derivative has nodules between the pelvic fin rays and the pelvic skeleton, which must therefore place *Indostomus* below the percoids.

Fishes in the series Atherinomorpha typically have a caudal fin skeleton which originates on one supporting centrum (as is the case in the majority of the Acanthopterygii). The caudal skeleton of *Indostomus* conforms to this pattern although the separate hypurals have fused up into one plate. This is possibly only to be expected because of the minuteness of its caudal skeleton.

There are some interesting trends within the suspensoria of some of the Atherinomorph families which may throw some light on the origin of the peculiar suspensorium of *Indostomus*. In the family Isonidae (Rosen, 1964) the autopalatine is greatly reduced and the endopterygoid is absent. This reduction in size and number of suspensorial bones has been continued further in *Indostomus*. The suspensorium and the jaws of the family Adrianichthyidae are of some interest. In many species of atheriniform fishes the upper jaw is protractile, but not in the Adrianichthyidae. There the maxilla is firmly joined to the upper edge of the premaxilla. The ethmoid is very large and has lost the disc-like appearance found in most atheriniforms. In these two respects it offers a parallel with *Indostomus*. The resemblance could go even further. In the adrianichthyids the lower jaw is of normal length and only the autopalatine links the upper jaw with the quadrate. If the proportions of the jaws and snout were altered to the proportions of those of *Indostomus*, a suspensorium very like that of *Indostomus* would result. This is pure hypothesis, but the adrianichthyids are a group of fish which satisfy the likely conditions for the pre-indostomid suspensorium.

If the lower jaw were elongated to articulate behind the eye, the autopalatine is already in position to elongate whilst keeping the upper jaw and quadrate tied together. As the quadrate is now behind the orbit and the lower jaw articulation almost vertical, there is no room for a large endopterygoid which could well disappear leaving just the hyomandibular, quadrate and symplectic to form the vertical column between the lower jaw and the braincase. The suspensorium of *Xenopoecilus* does not fit exactly into the appropriate pattern because the metapterygoid is now absent, yet is present in *Indostomus*, and although I have referred to the large suspensorial bone in *Indostomus* as the " pterygoid ", it could possibly be the autopalatine.

So, within the Atheriniformes there exist possible plans from which some of the characters of *Indostomus* could have evolved. It must, though be borne in mind that it is highly unlikely that the Adrianichthyidae have the basal suspensorial pattern of the order, and also that convergence could play a large part in the production of peculiarly modified suspensoria for somewhat similar jaws.

Parenthetically, it must be mentioned that the suspensorium of the ammodytoid *Hypoptychus dybowskii* (Gosline, 1963) is not unlike that of *Indostomus*. It differs mainly in having both the ectopterygoid and the palatine forming the lath in front of the quadrate and in the presence of a normal palato-maxillary connection. The jaws of *Hypoptychus* are approximately equal in length which suggests that this unusual pattern of suspensorium is not obviously related to the disposition of the snout and jaws and may well have occurred independently within the neoteleostei.

The Atheriniformes have the following features which differ from those in *Indostomus*.

1. A much higher number of vertebrae
2. No dorsal spines, and rarely a spiny first dorsal fin
3. Pelvic girdles with a long lateral spur
4. No trace of bony armour
5. Four pectoral pterygials, recessed within the scapulo-coracoid margin
6. Nasal bones usually present
7. A different arrangement of the upper pharyngeal tooth plates
8. Unarmed opercular bones

This makes the inclusion of *Indostomus* within the atherinomorph series unlikely. Little is known about atherinomorph ancestors, but the group evolved in the freshwaters of Asia, the area in which *Indostomus* now lives.

It is now necessary to try and fit *Indostomus* into the lower reaches of the Percomorpha series of the Acanthopterygii.

The order Lampridiformes contains the remarkable fish *Stylophorous chordatus* whose anatomy was described by Regan (1924). The most significant feature is the long mandible which in elongating backwards has carried the quadrate to a position behind the hyomandibular so that the suspensorium is angled forwards. The hyomandibular, quadrate and symplectic form a narrow column which is angled the opposite way from that in *Indostomus*. In *Stylophorous* the ecto-, endo- and metapterygoid bones are reduced to splinters between the quadrate and the hyomandibular. The autopalatine is a rod-like bone in a normal position but distant from the pterygoids. The premaxillae have large ascending processes and the mouth is highly protrusile. This elongated mandible is not universal amongst the Lampridiformes, but the modifications of the suspensorium form an interesting comparison with the situation in *Indostomus*. The presence of a basisphenoid, an orbitosphenoid, parietals, the dermopterotic-frontal contact which excludes the dermosphenotic from the skull roof, the high vertebral number long based dorsal fins without true spines and the absence of dermal armour are some of the many features which do not suggest any close relationships between the Lampridiformes and *Indostomus*. It is however, worth noting that three pectoral pterygials are common in that order.

Indostomus is far too specialized to be associated with the Beryciformes and their early offshoot the Zeiformes (Patterson 1964). Any relationship with the Synbranchiformes and Channiformes can be dismissed.

The order Scorpaeniformes is suspected by Greenwood *et alii* (1966) of being polyphyletic, but typically these fishes have the second suborbital bone contacting the preoperculum and a caudal skeleton consisting of two plate-like hypurals sutured to the terminal half centrum. The family Agonidae contains armoured forms which have retained the ribs and an unmodified caudal skeleton. Despite the precedent in the dermal armour of the Agonidae, the Scorpaeniformes are a fairly well defined order which, if any stock underwent reduction would be unlikely to produce the indostomid facies.

This leaves two small orders to consider, the Dactylopteriformes and the Pegasiformes.

The only point of similarity between the Dactylopteriformes and *Indostomus* is that both possess a low number of vertebrae, 22 in the former and usually 21 in the latter. The osteology is otherwise substantially dissimilar (Allis 1909).

The Pegasiformes are as much a problem as is *Indostomus*. *Pegasus* has never been described in detail, Jungersen (1914) has only given a brief account of the fish and from this one may gather that *Pegasus* is, like *Indostomus*, in an apparently isolated position.

The Paracanthopterygii is a superorder of fishes which, in the words of its definers, Greenwood *et alii* (1966) " represents a spiny finned radiation more or less comparable morphologically with that of the superorder Acanthopterygii ". Rosen and Patterson (1969) have shown that many of the acanthopterygian features of the Paracanthopterygii are lost during the evolution of the superorder.

The majority of the species included in the five component orders are marine, but the most primitive order the Percopsiformes is now confined to the fresh waters of the new world. Rosen and Patterson (1969) have shown that the superorder is monophyletic but contains two lineages : the percopsid-gadid lineage and the batrachoid-lophiid-gobiesocid lineage. The most trenchant characters separating the Paracanthopterygii from the Acanthopterygii are the presence of a levator maxillae superioris muscle and a second free ural centrum in the caudal fin skeleton. During the evolution of the batrachoid-gobiesocid lineage these two characters were modified and are absent in the gobiesocids, nevertheless a multitude of less trenchant characters links the batrachoids to the gobiesocids.

The Gobiesociformes are highly specialized fishes, as is *Indostomus*, and comparison of the characters of *Indostomus* with the trends within the batrachoid line that produced the gobiesocid facies reveals a number of similarities. Many of these can be explained by convergence and parallelism, some characters are of much less significance than others but whether convergence and/or parallelism can explain the particular combinations of characters present in both is something that will have to be argued when our knowledge increases.

Characters and trends present in the batrachoid lineage and in *Indostomus* are

1. Flattened skull roof
2. Fusion of parietals with epiotics
3. Autosphenotics flare forward

4. Absence of an intercalar
5. Horizontal alignment of the occipital condyles
6. Infraorbital series reduced to the lachrymal which lacks a suborbital shelf
7. Reduction of the pterygoid series
8. Hyomandibular and preopercular in intimate contact
9. Upper hypohyal elongated and lying over the cerataohyal
10. Six branchiostegal rays
11. Upper end of preopercular well below hyomandibular head
12. Posterior margin of opercular excavated
13. Caudal skeleton (in gobiesocids) fused up without a free parhypural
14. Pectoral radials enlarged
15. Coracoid with a posteroventral process
16. Spinous anterior dorsal fin rays
17. Rounded caudal fin
18. Scales absent
19. No orbito- or basisphenoids
20. Subopercular slender and directed towards the upper corner of the opercular
21. Adductor arcus palatini across the floor of the orbit
22. Pelvic fins subthoracic and with reduced number of rays
23. Upper and lower jaw teeth fail to occlude completely.

Some of these characters need further qualification. 1, 5, 12 and probably 8, all seem to be related to the flattening of the skull. Rosen and Patterson (1969) pointed out that in paracanthopterygians the exoccipital condyles tend to lie alongside the basioccipital condyle, whereas in the acanthopterygians they tend to lie above the basioccipital condyle. This is mechanically necessary in fishes which raise their heads, a practice found in both *Indostomus* and the paracanthopterygians. In the Scopraeniformes *Hoplichthys langsdorfii* the exocciptal flanges are level with the basioccipital condyle ; in *Platycephalus insidiator* and *P. japonicus* they are only a little higher, and fail to meet medially above the basioccipital condyle. A similar situation is found in the perciformes *Gymnodraco acuticeps* and *Parachaenichthys georginaus.*

Number 13, the fused caudal skeleton, is another character which needs some comment. A caudal skeleton which has had all its components parts fused into a single hypural plate supported on one centrum is found in advanced perciforms as well as in the Paracanthopterygii and the Gasterosteiformes. In the case of *Indostomus* the evidence afforded by the second pre-ural neural spine (Patterson, 1968, Rosen and Patterson, 1969) cannot be called upon, because the neural arches of all the caudal vertebrae of *Indostomus* have fused with the dermal scutes. Most perciforms in which the caudal skeleton is fused typically have an autogenous parhypural whilst in the Gobiesociformes the parhypural is fused with the hypural plate. In the scombrids, where the parhypural is in some species fused with the hypural plate, a well developed parhypural process is evident. In the Gasterosteiformes (with the exception of the highly reduced caudal skeletons of the Syngnathidae) the parhypural, when fused, is usually obvious in alizarin preparations. The absence of an autogenous parhypural in *Indostomus* suggests a real affinity with the Gobiesocids, because although the caudal skeleton is as fused as it is in the syngnathids, the caudal fin plays a much greater role in the locomotion of the fish. In other words the consolidation of the urophore elements is more likely to be the result of a phyletic trend (as in the batrachoid-gobesocid line) than of reduction resulting from a trend to develop a prehensile tail and lose the caudal fin as in the Syngnathidae.

The excavated hind margin of the opercular (12), is a feature that is also present in the Scorpaeniformes (a group that seems to have several paracanthopterygian trends) but the very spiny type of opercular present in *Indostomus* and batrachoids like *Opsanus tau* (with the consequent excavations of the rear margin) does not seem to be repeated anywhere else in quite this form. None of the batrachoids have as many pungent spines as does *Indostomus*.

Characters 2, 4, 6, 7, 10, 13, 14, 16, 17, 18, 19, 20 and 23 are far from rare in the Acanthopterygians and their significance would seem to lie in their particular combination in one group of fishes.

Characters 3,9, 11, 15, 21 and 22 must indicate either that *Indostomus* has some affinity with the batrachoid lineage of the Paracanthoptergyii or that it exhibits a remarkable degree of convergence in these rather specialized features.

The jaws of *Indostomus* are highly aberrant but would seem to conform to the " maxillary rotation " style present in the higher Paracanthopterygii. Within the batrachoid lineage when the levator maxillae superioris muscles are absent, no muscles insert on the maxillae and the rotation of the upper jaw in under the sole control of the depression of the lower jaw.

One would expect that the peculiar ethmoideum of *Indostomus* would be too specialized to reveal any affinities with more orthodox fishes. The only points worth mentioning in this context are that in *Opsanus beta* the vomer is fused with the ethmoideum (Rosen and Patterson, 1969), and that in *Opsanus tau* at least (see fig. 263 in Gregory, 1933) the physical disposition of the ethmovomer block and the pterygoquadrate bars are much the same as they are in *Indostomus*.

Primitive Paracanthopterygian features present in *Indostomus* include the following :

1. Absence of a supra-temporal fossa
2. Two openings to the pars jugularis
3. Parasphenoid-pterosphenoid contact
4. No pelvic spine.

Apart from the specializations of the snout and jaws, there are several important differences between *Indostomus* and the paracanthopterygians. The following are characters of *Indostomus* which are not found in the more highly evolved paracanthopterygians (although some are present in the Percopsidae).

1. A strong ventral process of the posttemporal
2. Short hypobranchials
3. A distinct gap between the epibranchials 3 & 4
4. No reduction of the basibranchials
5. No ascending processes on the premaxillae
6. Considerable reduction of the lateral line system
7. Absence of ribs
8. Dermal armour.

It seems then that *Indostomus* contains a mosaic of a few features that are primitive to fishes of the level of basal paracanthopterygians, several features also found in members of the batrachoid-lophiid-gobiesocid lineage and a few characters *sui generis*. The presence of the characters peculiar, in this combination, to the batrachoid-gobiesocid lineage make it less likely (but not impossible) that a similar combination could be found in acanthopterygian fishes.

The balance of evidence suggests that *Indostomus* could have evolved from one of two species. It could have evolved from a species just on the paracanthopterygian side of the paracanthopterygian-acanthopterygian dichotomy and then have evolved along a line somewhat parallel to the batrachoid-gobiesocid line to produce a fish with the short dorsal and anal fins and the few rayed caudal fins as in the Gobiesociformes. The other possibility is that *Indostomus* evolved from a species somewhere on the line leading to the gobiesocids. The fact that the most precise characters are those shared with the more highly evolved paracanthopterygians is some evidence for this.[1] The fact that the gobiesocids are marine littoral forms found in the Indian Ocean does not contradict this when Prashad's and Mukerji's views on the origin of Lake Indawgyi are taken into account. The presence of the primitive features could then, in some cases be explained by secondary reduction and simplification.

Much of this discussion is, of necessity, speculative, but the balance of evidence leads me to consider *Indostomus paradoxus* to be the only species of a new Paracanthopterygian order ; order Indostomiformes, which shows some affinities with the Batrachoidiform-Gobiesociform lineage of that superorder.

The diagnosis of the order Indostomiformes is essentially that of the species viz. small freshwater fishes from Upper Burma, the body has a complete dermal armour covering ; the head is depressed and is mobile ; the pterygoid series of bones is reduced in number ; the upper jaw is not protrusile ; the lower jaw is long ; a series of isolated spines is present in front of the dorsal fin; the dorsal and anal fins are short based and opposite each other ; the pelvic fin contains fin rays with cartilaginous nodules at their bases ; there is no pelvic fin spine.

SUMMARY

1. The anatomy of *Indostomus paradoxus* is described.
2. A new order-INDOSTOMIFORMES is proposed to contain this single species.
3. It is suggested that the order Indostomiformes be placed within the superorder Paracanthopterygii and probably near the Gobiesociformes.

ACKNOWLEDGEMENTS

I am very pleased to be able to thank Dr. Alan Tubb of the F.A.O. in Thailand for providing the specimens of *Indostomus* and so generously letting me use his unique observations on the living fish.

Drs. P. H. Greenwood, C. Patterson and E. Trewavas have helped immeasurably

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[1] Whilst in the realms of speculation I am tempted to compare the behaviour of captive *Indostomus* in leaping out of the water and sticking onto the glass (presumably by a combination of surface tension and a flattened belly—see Appendix) with the trend to develop a sucking disc in the Gobiesociformes.

in putting this work on paper in an orderly fashion and eliminating many of my mistakes. Needless to say any remaining errors are all my own work.

To all these people I gratefully offer my thanks.

APPENDIX I

Based on notes made on the behaviour of the living *Indostomus* by Dr. Alan Tubb

Notes on *Indostomus*

About 140 specimens collected from a small creek entering the west side of Lake Indawgyi were brought alive to Rangoon and installed in two small (10 gallon) aquaria, on 3 April 1956.

One aquarium tank contained a pure stock of *Indostomus*, about 110 individuals, the other contained a variety of small *Barbus* spp., *Platypoecilus* and *Xiphophorus* hybrids.

Both tanks had sand on the bottom and were planted with clumps of *Cabomba* and dwarf *Sagittaria*.

In the community tank, the older inhabitants spent some time chasing and nipping at the *Indostomus*, without however doing any obvious damage, and after two days the enlarged community settled down and no further attacks occurred.

The *Indostomus* is quiet in behaviour, and generally slow-moving. Normal movement is effected almost wholly by means of the pectoral fins which maintain a constant rapid fluttering movement, even when the fin is apparently completely at rest. When alarmed, these fish move with remarkable speed, apparently using the relatively large fanshaped caudal fin. The dorsal and anal fins are usually folded along the body, but may be fully spread when the fish is moving slowly, with no apparent purpose, or when resting in an inclined position close to an ascending strand of vegetation. The dorsal and anal fins, together with the tiny pelvics are used as " brakes " and are widely spread to retard forward motion. They and the caudal fin are often spread when the fish is "hanging " in the water, presumably to provide an increased resisting surface.

The *Indostomus* appears to feed entirely on animal food, but will only take live organisms. In the aquarium, they fed readily on small tubificid worms which were scattered over the surface of the water and allowed to sink slowly to the bottom. Only rarely were worms actually sinking taken by the fish. In almost all cases, the worms fell to the bottom and were then taken.

When approaching a food item, the *Indostomus* moves very slowly, all fins depressed except the pectorals, which maintain their constant fluttering motion. When close to the food organism, the fish rolls gently over to one side, either right or left. In the case of a worm protruding from the sand, the roll may be sufficient to place the transverse axis of the body at 90° to normal. The final millimetre of movement is accomplished by a sudden dart (the jaws are not protrusible) and the food item snapped up. If the worm is deeply imbedded in the sand, the fish, having gripped the exposed portion, wriggles violently backwards, and usually succeeds in withdrawing the worm from its tube.

Colonial protozoans growing on the aquarium walls or on the vegetation are taken in a similar manner, the degree of rolling depending on the situation of the colony. In this latter case, the withdrawal by the fish is steady, and usually only a few millimetres.

Normally there appears to be little belligerence between individuals, although actual shoaling does not occur, each fish moving independently of other members of the community. Occasionally, however, a fish seems to establish a kind of temporary " territory ". These individuals, by their more slender form, and the absence of the whitish or greenish mass visible through the translucent walls of the abdomen of other less slender specimens, are probably males.

In the cases observed, the " territory ", which does not appear to exceed in diameter twice the total length of the fish, is maintained only for brief periods, rarely more than 15 minutes, but during this time, all other members of the species which infringe the boundary are driven off, although no damage appears to happen to the invader.

Despite its dermal armature, the fish is surprisingly flexible in life, and can bend in an almost complete circle, the snout approaching within a few millimetres of the caudal fin. The most remarkable feature, however, is the flexibility of the " neck ". It is one of very few fishes known to the writer, which can actually " raise its head ". The free anterior vertebrae, permit a vertical flexure of the head to an angle of about 10° from the main axis of the body. Lateral and ventral flexures of about the same order of magnitude also occur.

In the tank containing only *Indostomus* the fish showed a strong tendency to assemble in the darkened areas, particularly, a number would cluster, heads upward, on the inner surface of the angles of the tank, where they were sheltered from the direct front lighting. Not all followed this habit, many spending the great part of the day lying flat on the bottom, or resting head upwards at an angle of 30–75° among the vegetation. These resting periods appeared to be prolonged, although it was not possible to be sure that any one individual remained in the same place for an extended period.

A peculiar reaction was noted when the fish were unusually disturbed, either when the glass of the tank was being cleaned, or occasionally when the " mulm " was being siphoned from the bottom. Most of the fish would dart wildly about, producing a noticeable clicking sound as their bony snouts bumped against the glass walls of the tank. A few, however, would leap clear of the surface and adhere to the upper part of the glass, 1 or 2 centimetres above the water. They failed to respond to a gentle touch, remaining quite immobile, and either had to be gently pushed back into the water, or allowed to remain until they flipped back again of their own accord. One specimen was observed to remain sticking to the glass for 4½ minutes before wriggling into the water again. They apparently suffered no damage from this exposure.

In the community tank, the *Indostomus* paid little attention to the other species, simply moving slowly aside as another fish approached. The current induced by the sudden sweep of the caudal fin of a larger fish often tumbled these extremely light creatures over and over, but did not appear to cause them a great deal of alarm.

The respiratory movements are worthy of note. The mouth remains open constantly, except when food is actually being ingested, and the gill covers are spread outwards, forming a narrow frill one each side of the head. The gills are thus partly exposed and are clearly visible from any position behind to the posterior edge of the gill covers, or from below, the branchiostegals and their connecting membranes also being widely spread. There is a steady rapid pulsation of the isthmus and connected membranes, but as there does not appear to be any inner postlabial skin fold to serve as an oral valve, such as that found in certain of the siluroids and other fishes, it is difficult to avoid the impression that the respiratory current is not, in part at least, induced by the continuous fluttering of the pectoral fins. When " stalking " its food, the *Indostomus* depresses the otherwise extended opercles and branchiostegals and the pulsation of the isthmus appears to cease entirely.

The breeding of this fish has not yet been observed, but several specimens, apparently females, showed evidence of gonadal development during late June 1956. These fish became markedly more robust in appearance and, through the translucent body walls, the development of the ovaries was readily observable. The first obvious stage was the appearance of a pale creamy mass occupying about half the length and about one third of the volume of the abdominal cavity, extending from opposite the first dorsal spine to the vent. In some of the fish under observation, this mass later assumed a delicate jade green color, and although the length did not appear to increase, the distension of the abdomen became more marked. In the noticeably more slender specimens, and particularly in those showing the temporary " territory " habit mentioned above, no such evidence or gonadal development was observed.

When captured, all specimens were generally dark to dusky brown the fins showing the transverse banding mentioned by Prashad and Mukerji (loc. cit. p. 221). In the aquarium tanks however, in the clear water and under the relatively bright light conditions, most specimens rapidly became a very light, honeybrown color and the fin patterns were reduced to extinction. Dorsally, on each side of and close to the mid line were four bright golden squares, situated at the interspaces between the dorsal spines, i.e. on the 4–7 rings. Some specimens occasionally become somewhat darker in color, when indistinct transverse bands of cloudy black appear, apparently coinciding with the rings and extending from the anterior (scapular of Prashad and Mukerji) to the first caudal ring. On such individuals, the transverse banding of the fins, particularly the caudal fin, becomes evident.

KEY TO FIGURES

an	angular	mpt	metapterygoid
anf	anterior nostril	mx	maxilla
ar	articular	na	neural arch
bb	basibranchial	op	operculum
bo	basioccipital	pmx	premaxilla
bp	body plate	pnf	posterior nostril
br	branchiostegal ray	pop	preopercular
c	centrum	pro	prootic
cb	ceratobranchial	ps	parasphenoid

ch	ceratohyal	pt	pterotic
cl	cleithrum	ptm	posttemporal
co	coracoid	pts	pterosphenoid
d	dentary	pty	pterygoid
dpt	dermal part of pteroticum	q	quadrate
dsp	dermal part of sphenoticum	r	pectoral pterygial
Dsp	dorsal spine	sa	sesamoid articular
e	ethmoid	sc	scapular
eb	epibranchial	scp	scapular foramen
eh	epihyal	scl	supracleithrum
epo	epiotic	se	supraethmoid
ex	exoccipital	so	supraoccipital
f	frontal	sop	suboperculum
hb	hypobranchial	sp	sphenotic
hm	hyomandibular	sy	symplectic
hy	hypural	tp	transverse process
ih	interhyal	tpf	facet on transverse process
iop	interoperculum	uh	upper hypohyal
la	lachrymal	up	upper pharyngeal
le	lateral ethmoid	ur	urohyal
lh	lower hypohyal	v	vertebra
lig	ligament	vo	vomer
llc	lateral line canal		

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BY

GEOFFREY PALMER

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NEW RECORDS, AND ONE NEW SPECIES, OF TELEOST FISHES FROM THE GILBERT ISLANDS

By G. PALMER

An interesting collection of marine fishes, which has now been presented to the museum, was made in 1962 by Mrs. M. J. Cooper, whilst she was living at Betio, Tarawa in the Gilbert Islands.

Randall (1955) in his report on the fishes of the Gilbert Islands, stresses the fact that there seem to be few species endemic to this group of islands, the majority of those found in this area being common to many of the oceanic islands of the tropical Pacific. In particular, the fauna is very similar to that of the Marshall Islands, some of the icthyofauna of which has been dealt with by Schultz et al (1953 and 1960). About 400 species were recorded by Randall, some of which are represented in the present collection. Despite its comparatively small size of 297 specimens, the present collection cosists of 75 species, 21 of which, including the new species, are listed as new records for the Gilbert Islands. These are indicated by an asterisk. In a number of instances live colour notes were made by Mrs. Cooper and these have been included under the appropriate species.

APODES

MURAENIDAE

Echidna zebra (Shaw)

Gymnothorax zebra Shaw, 1797, *Nat. Misc.*, **9**: pl. 322
B.M. No. 1969.8.26.1–3.

3 specimens, 152–324 mm. in length. Taken off reefs at Bairiki, Tarawa.

The smallest example has 21 complete light bands encircling the body, the number of these apparently increasing with size, as the other two larger specimens have 25 and 39 bands respectively. Between the complete bands are a varying number of partial bands or spots.

Echidna nebulosa (Ahl)

Muraena nebulosa Ahl, 1789, *Spec. ichthyologicum de Muraena et Ophichtho* (Thunberg): 7. pl. right fig.
B.M. No. 1969.8.26.4–12.

9 specimens, 87–393 mm. in length, from bomb-crater tide-pool, Tarawa.

The teeth in the small examples are less molar-like than are those in the larger fish.

The 315 mm. eel is anomalous in having the tubes of the anterior nostrils united, although the nasal apertures are separate.

Echidna ? leucotaenia Schultz

Echidna leucotaenia Schultz, 1943, *Bull. U.S. natn Mus.* **180**: 22.
B.M. No. 1969.8.26.13–14.

2 specimens, 39 and 40 mm. in length. Taken off Tarawa reefs.

Both specimens show the whitish snout and lower jaw, as well as the white margin on the median fins, which are said by Schultz to be characteristic for this species.

* *Pseudechidna brummeri* (Bleeker)

Muraena brummeri Bleeker, 1858, *Natuurk. Tijdschr. Ned. Indie* **17**: 137.
B.M. No. 1969.8.26.15.

1 specimen, 350 mm. in length, from Tarawa lagoon.

Trunk 190 mm., tail 160 mm. Greatest depth 11 mm. Head 28 mm. Greatest height of dorsal fin 5 mm. Median fins well-developed, the height of the dorsal in the posterior part of the tail region being as high as the depth of the body. Dorsal, caudal and anal fins with a marginal white band. Colour of body an overall light brown with the anterior pores of the head and lower jaw a dark brown, as are the tubes of the anterior nostrils. Teeth conical, depressible, a double row in the maxillary series, those of the inner row being the larger. A single row in the intermaxillary series, with three mesial teeth. Vomer with a single row of 6 or 7 teeth. Teeth of the lower jaw in a single series. This species was not recorded by Schultz (1953) from the Marshall and Marianas Islands and appears to be a new record for the Gilbert Islands.

Murenophis pardalis (Temminck & Schlegel)

Muraena pardalis Temminck & Schlegel, 1846, *Fauna japonica Pisces* Pt. 5: 268 pl. 119.
B.M. No. 1969.8.26.33.

1 specimen, 132 mm. in length from Tarawa lagoon.

Colour brownish, with prominent white spots which tend to coalesce to form vertical white lines.

Gymnothorax picta (Ahl)

Muraena picta Ahl, 1789, *Spec. ichthyologicum de Muraena et Ophichtho* (Thunberg): 8.
B.M. No. 1969.8.26.16–26.

11 specimens, 72–474 mm. in length, taken from Tarawa lagoon.

Gymnothorax petelli (Bleeker)

Muraena petelli Bleeker, 1856, *Natuurk. Tijdschr. Ned. Indie* **11**: 84.
B.M. No. 1969.8.26.27.

1 specimen, 112 mm. in length, from Tarawa lagoon.

Gymnothorax rüpelli (McClelland)

Dalophis rüpelliae McClelland, 1845, *Calcutta J. nat. Hist.* **5**: 213.
B.M. No. 1969.8.26.28–32.

5 specimens, 50–212 mm. in length, from Tarawa lagoon.

The three smallest examples have a line of solid, dark pigment running longitudinally along the ventral surface, linking the dark rings.

Gymnothorax thyrsoideus (Richardson)

Muraena thyrsoidea Richardson, 1844, *Zool. Voy. "Sulphur"*—Fishes: 111.
B.M. No. 1969.8.26.35–38.

4 specimens, 202–270 mm. in length, from Tarawa lagoon.

Gymnothorax undulata (Lacepède)

Muraenophis undulatus Lacepède, 1803, *Hist. nat. Poissons* **5**: 629, 642, 644 fig. 2.
B.M. No. 1969.8.26.39–40.

2 specimens, 114 and 302 mm. in length from Tarawa lagoon.

It is with some hesitation that the 114 mm. specimen is included in this species. Colouration in life was stated to have been pale brown, mottled with darker brown.

Gymnothorax favaginea Schneider

Gymnothorax favagineus Schneider, 1801, *Syst. Ichth. Bloch.*: 525.
B.M. No. 1969.8.26.41–42.

2 specimens, 52 and 62 mm. in length from Tarawa lagoon.

These two specimens have the snout and the distal margins of the fins white. The smaller of the two is very dark and shows only light interspaces on the dorsal half of the body.

Gymnothorax fimbriata (Bennett)

Muraena fimbriata Bennett, 1831, *Proc. zool. Soc. Lond.* Pt. 1: 168.
B.M. No. 1969.8.26.43–44.

2 specimens, 159 and 273 mm. in length. Tarawa.

The smaller specimen was taken on the reef off Tarawa at night. The larger was taken from Tarawa lagoon over sand and rock. Live colours are stated to have been a cream background mottled with brown.

Gymnothorax flavimarginata (Rüppell)

Muraena flavimarginata Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 119, pl. 30, fig. 3.
B.M. No. 1969.8.26.45–51.

7 specimens, 117–283 mm. in length, taken on the outer reef, Tarawa.

Live colour brown, mottled with darker brown. A bright greenish margin to dorsal fin and around caudal.

Gymnothorax sp.

B.M. No. 1969.8.26.52–54.

3 specimens, 52–80 mm. in length, taken in Tarawa lagoon.

I have been unable to assign these specimens to any particular species.

* ***Uropterygius leucurus*** Snyder

Uropterygius leucurus Snyder, 1904, *Bull. U.S. Fish. Comm.* **22**: 521, pl. 6 fig. 12.
B.M. No. 1969.8.26.55–65.

11 specimens, 87–123 mm. in length. Taken on Betio, Tarawa at low water in a tide-pool with rotenone.

This appears to be a new record for the species from the Gilbert Islands. The type was taken in the Hawaiian Islands, and more recently has been recorded by Schultz in Schultz et al (1953) from the Marshall and Marianas Islands.

Trunk 42 mm., tail 45 mm. About 94 pores in the lateral line.

Colour in alcohol overall brownish. On the smaller specimens there are some 70 alternating vertical bars, sometimes incomplete, of brown and white. These are visible from the rictus of the jaws back to the end of the body.

Uropterygius micropterus (Bleeker)

Muraena micropterus Bleeker, 1852, *Natuurk. Tijdschr. Ned. Indie* **3**: 298.
B.M. No. 1969.8.26.66–69.

4 specimens, 200–233 mm. in length. Taken at Bairiki, Tarawa on outer reef, close inshore in tide-pools. Very common in this area.

I follow Randall (1955) in considering this to be distinct from *U. marmoratus*, although some authors believe these two species to be synonymous.

The maxillary teeth are in two series, the inner being two to three times as long as those of the outer row. They are canine-like, depressible and extend the whole length of the maxillary. The mandibular teeth are also in two series, the inner row again being the longer and extending almost to the rictus of the jaws. There are 6–7 vomerine teeth in a single series.

Live colour is stated to be white, speckled with greyish-black. Colour in alcohol is a greyish-white, speckled with darker markings along the dorsal side of the body. Ventral surface an unrelieved greyish-white.

Uropterygius marmoratus (Lacepède)

Gymnomuraena marmorata Lacepède, 1803, *Hist. nat. Poissons* **5**: 648.
B.M. No. 1969.8.26.70–77.

8 specimens, 40–460 mm. in length, from Tarawa lagoon.

* ***Anarchias allardicei*** Jordan & Starks

Anarchias allardicei Jordon & Starks, *in* Jordan & Seale, (1905) 1906, *Bull. U.S. Bur. Fish.* **25:** 204, fig. 9.
B.M. No. 1969.8.26.68.

1 specimen, 73 mm. in length. Taken in bomb-crater tide-pool on the southern reef, Betio, Tarawa.

This specimen is almost certainly a young example of *A. allardicei.* It is of a plain, darkish brown colour, much lighter around the caudal fin. The snout and lower jaw are very pale. The tooth pattern agrees very closely with the diagram in Schultz in Schultz et al (1953) for this species. Previously recorded from Samoa and the Marshall and Marianas Islands, it is not surprising to find that it occurs in this region, from which it has not previously been recorded.

OPHICHTHIDAE

Randall (1955) follows Myers and Storey (1929) and Gosline (1950) including in this family the genus *Muraenichthys.* I have followed this course here.

Myrichthys maculosus (Cuvier)

Muraena maculosa Cuvier, 1817, *Règne Animal* (*1st. Ed.*) **2:** 232.
B.M. No. 1969.8.26.79–80.

2 specimens, 98 and 265 mm. in length. Taken on the outer reef at Bairiki, Tarawa, on sand with rocks.

The live colour of the larger specimen was a deep cream, with reddish-brown spots. There are 28 of these in a lateral series, with a few smaller ones along the dorsal edge of the body in the interspaces. The smaller example shows only a few groups of melanophores along the sides of the body.

Myrichthys colubrinus (Boddaert)

Muraena colubrina Boddaert, 1781, *Neue nord. Beytr.* **2:** 56, pl. 2 fig. 3.
Ophisurus fasciatus var. *semicincta* Bleeker, 1864, *Atlas ichthyol. Indes orient. Neerl.* **4:** 64.
Chlevastes elaps Fowler, 1912, *Proc. Acad. nat. Sci. Philad.* **64:** 13.
B.M. No. 1969.8.26.81–82.

2 specimens, 398 and 628 mm. in length, taken off the reef at night, Betio, Tarawa.

Schultz in Schultz et al (1953) states that the species *M. semicinctus* (Bleeker) and *M. elaps* (Fowler) are distinct from *M. colubrinus,* primarily on the form and completeness of the vertical bands, with the presence or absence of additional dark spots or markings in the interspaces. Randall (1955) and Smith (1962), however, consider these two forms to be synonymous with *M. colubrinus.* It may be noted that of the two specimens listed above the smaller keys out, according to Schultz, as *semicinctus,* whilst the larger represents *elaps.* Smith (1962) gives an illustration showing both forms under the name *colubrinus.* Here again, the smaller of these is a *semicinctus* according to Schultz, whilst the larger shows the wider bands and many dark spots and partial bands in the interspaces, of an *elaps.*

Callechelys melanotaenia Bleeker

Callechelys melanotaenia Bleeker, 1864, *Atlas Ichth. Ind. Neerl.* . . . **4:** 66, pl. 193 fig. 2.
B.M. No. 1969.8.26.83–86.

4 specimens, 449–543 mm. in length. Taken with rotenone in bomb-crater tide-pool, Betio, Tarawa.

Callechelys sp.

B.M. No. 1969.8.26.87.

1 specimen, 86 mm. in length, taken in bomb-crater tide-pool, Betio, Tarawa.

This specimen shows no colour pattern, other than a few circular groups of melanophores scattered along the sides of the body.

* ***Muraenichthys macropterus*** Bleeker

Muraenichthys macropterus. Bleeker, 1857, *Act. Soc. Scient. Ind. Neerl.* **2:** 91.
B.M. No. 1969.8.26.88.

1 specimen, 235 mm. in length, taken in Tarawa lagoon.

Although this species has been recorded from the Tuamotu Archipelago and from the Marshall and Marianas Islands (Schultz in Schutz et al 1953), it has not previously been listed from the Gilbert and Ellice Islands.

Greatest depth 7 mm.; head length 24 mm.; trunk (from snout tip to vent) 90 mm.; length of tail 143 mm.; origin of dorsal fin 39 mm. anterior to vent.

Live colour was a sandy pink, with pale fins. Colour of preserved specimen a light brown.

Muraenichthys sp.

B.M. No. 1969.8.26.89.

1 specimen, 118 mm. in length. Taken in bomb-crater tide-pool on southern reef, Betio, Tarawa.

I am unable to assign a specific name to this specimen. Measurements are as follows: depth of body 3 mm.; head 12 mm.; trunk 43 mm.; tail 75 mm.; dorsal origin is 4 mm. in advance of vent. Maxillary and mandibular teeth in single series, vomerine teeth biserial.

Phaenomonas

Phaenomonas Myers and Wade, 1941, *Allan Hancock Pac. Exped.* **9:** 77, pl. 12.
B.M. No. 1969.8.26.90.

This genus has been known only from the type species, *P. pinnata*, taken off the Pacific coast of tropical America, notably from Colombia and Isabel Island, Mexico. The specimen reported on here is considered to be distinct from *P. pinnata* and is described below. It is necessary, also, to modify the generic diagnosis given by Myers and Wade by altering the statement concerning the length of the dorsal fin. The amended description is given herewith.

Body elongate, cylindrical, very wormlike. Head and trunk much longer than tail. A short, well-developed dorsal fin is present commencing on the head approximately half way between the snout and gill-opening; its entire length is not more than three times the head length. No pectoral or anal fins present. Snout blunt, lower jaw included. Eye small and almost hidden beneath skin, closer to angle of jaw than to tip of snout. Anterior nostrils tubular, on underside of snout. Posterior nostrils on underside of upper lip, the pore covered by a small membrane. Gill openings nearly vertical, low lateral. Teeth uniserial.[1]

* ***Phaenomonas cooperae*** sp. nov.

Fig. 1

HOLOTYPE: Brit. Mus. (Nat. Hist.) 1969.8. 26. 90. 513 mm. in length.
LOCALITY: Lagoon reef at Betio, Tarawa.

Body extremely elongate, cyclindrical. Tail ending in a blunt, conical point. Depth of body contained 128 times in total length. Tail very short, contained 2·3 times in length of head and trunk. Dorsal fin present, originating midway between tip of snout and gill-opening and extending back to above the 39th vertebra; it is 57 mm. long and almost 3 times the head length. No anal or pectoral fins. There are about 260 pores in the lateral line from above the gill-opening to the end of the tail. The anterior nostrils are tubular, placed on the underside of the snout. The posterior nostrils are under the edge of the upper lip, covered by a flap of skin, and lie below the posterior half of the eye. The eyes are small, about 1/3 snout length and almost completely hidden beneath the integument and probably virtually non-functional. The gill-openings are oblique, low lateral in position, their length of 3 mm. being equal to the width of the isthmus. Ventral surface of snout grooved, with an enlarged premaxillary tooth in the groove. Teeth uniserial. Maxillary teeth, as in *P. pinnata*, running in a straight line from posterior insertion to the head of the vomer. Vomerine teeth in a single row, widely spaced, about 5 in number. Only three premaxillary teeth present, one on either side of the groove in the snout and partially hidden by a flap of skin. An enlarged median tooth protruding from the groove itself. Mandibular teeth in a single row on either side, becoming smaller posteriorly. All the teeth are conical.

Colour in alcohol a sandy brown, with no trace of pigment.

Summary of counts and measurements. Total length 513 mm.; depth of body 4 mm.; head and trunk 357 mm.; tail 156 mm.; head 18 mm.; snout 3 mm.; eye 1 mm. Depth in length 128·25; head in trunk 19·8; tail in trunk 2·3; eye in snout 3; dorsal fin 3 times head length; length of dorsal fin 57 mm.; number of lateral line pores 260; number of vertebrae 270.

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[1] After this paper had gone to press, Dr. McCosker of the Scripps Institution of Oceanography informed me that he had 32 adult examples from the western Caroline Islands that appeared to be a new species of *Phaenomonas*, and offered some of this material to me for study. He also told me that Mr. Wayne Baldwin had obtained an adult specimen of this genus from Hawaii. For a full treatment of this genus, therefore, reference should be made to a joint paper which is to be published by Dr. McCosker and Mr. Baldwin.

Through the courtesy of the authorities of the Los Angeles County Museum, I have been enabled to examine the paratype of *P. pinnata*, which is 233 mm. in length. *P. cooperae* differs from the type species in having a proportionately longer dorsal fin, 3 times head length compared with less than head length; a larger number of lateral line pores, 260 as against 175, and the eye contained 3 times in snout as against 5–6 times in *P. pinnata*.

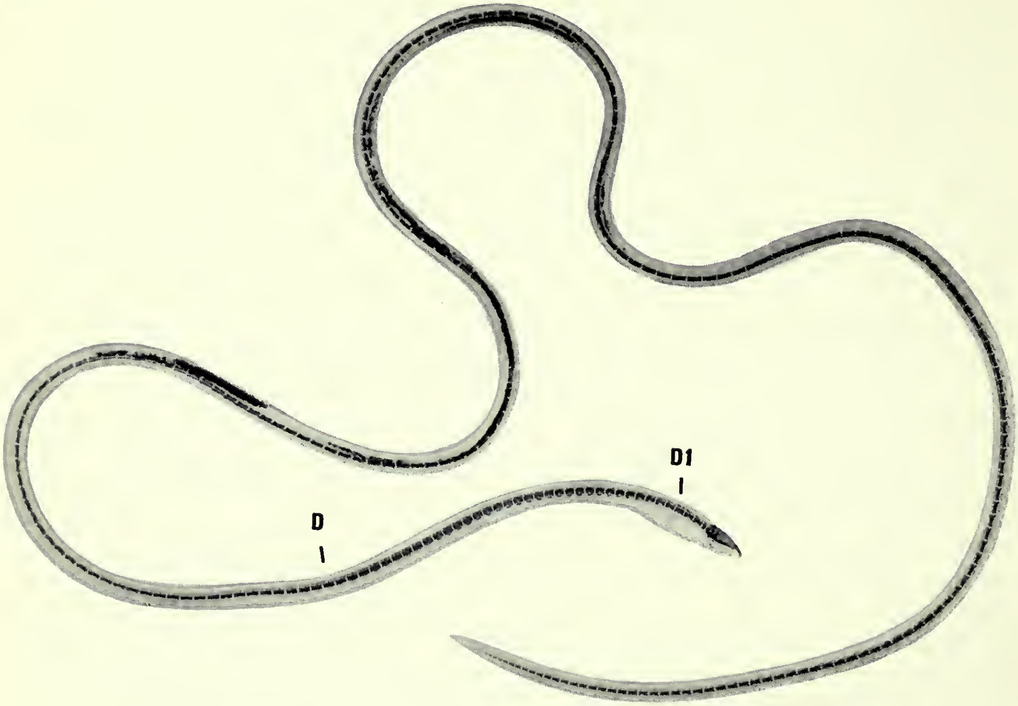

FIG. 1. X-ray of *Phaenomonas cooperae*. D–D1 = position of dorsal fin.

The species is named in honour of Mrs. Jane Cooper, without whose enthusiasm this collection would not have been made.

MORINGUIDAE

Randall (1955) states that he follows Gosline and Strasburg (1956) in classifying the worm eels. I am following the same course here, so that material which keyed out in Schultz (1953) as *M. abbreviata* and *M. macrocephala* is here listed as *M. macrochir*. P. H. J. Castle (in litt.) states that he is convinced from pore and vertebral counts that *M. macrochir* and *M. macrocephala* are identical.

Moringua macrochir Bleeker

Moringua macrochir Bleeker, 1855, *Natuurk. Tijdschr. Ned. Indie* **9**: 71.
Aphthalmichthys abbreviatus Bleeker, 1863, *Ned. Tijdschr. Dierk.* **1**: 163.
Aphthalmichthys macrocephalus Bleeker, 1863, *Ned. Tijdschr. Dierk.* **1**: 165.
B.M. No. 1969.8.26.91–125.

35 specimens, 144–368 mm. in length. Taken at Betio, Tarawa in bomb-crater tide-pools, with rotenone.

Colour in alcohol a uniform light yellowish brown. The number of lateral line pores from above the gill-opening to the end of the tail varies between 93–120.

Moringua javanica (Kaup)

Aphthalmichthys javanicus Kaup, 1865, *Cat. Apodal Fish. Brit. Mus.* 105, fig. 71.
B.M. No. 1969.8.26.126–129.

4 specimens, 340–740 mm. in length. Taken at Betio, Tarawa in bomb-crater tide-pool.

Colour in alcohol a light greyish brown. The number of lateral line pores varies from 138–148.

CONGRIDAE

* *Conger cinereus cinereus* Rüppell

Conger cinereus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 115.
B.M. No. 1969.8.26.130–131.

2 specimens, 538 and 735 mm. in length. Taken off Tarawa reefs at night.

These specimens represent a new record for the Gilbert Islands. The sixth infraorbital pore is above the rictus of the jaw. Pectoral fin with 15–16 rays. A black spot is present on this fin in both specimens.

According to Kanazawa (1958), this subspecies ranges through the Marshall, Phoenix and Christmas Islands, Palmyra, New Caledonia, Guam, Okinawa, Japan, the Philippines westward through the Indian Ocean, the Red Sea and the east and south coasts of Africa.

It is believed to be nocturnal in its habits and this is borne out by the fact that both these examples were taken at night.

HEMIRHAMPHIDAE

Hyporhamphus dussumieri (Val.)

Hemirhamphus dussumieri Valenciennes, 1846, *Hist. nat. Poissons* **19**: 33, pl. 554.
B.M. No. 1969.8.26.132–135.

4 specimens, 73–96 mm. in S.L. Taken in Tarawa lagoon.

In June, 1968, 3 additional specimens of this species, collected by Dr. D. N. F. Hall, were received from the same locality. These were 245–263 mm. in S.L.

SYNGNATHIDAE

Doryrhamphus melanopleura (Bleeker)

Syngnathus melanopleura Bleeker, 1858, *Natuurk. Tijdschr. Ned. Indie* **15**: 464.
B.M. No. 1969.8.26.136.

1 specimen, 48 mm. in S.L., from Tarawa lagoon.

SERRANIDAE

* **Epinephelus kohleri** Schultz

Fig. 2

Epinephelus kohleri Schultz, 1953, *Bull. U.S. Nat. Mus.* No. 202 Pt. 1: 336.
Serranus cyanopodus Richardson 1846. Whitehead, 1969, *Bull. Br. Mus. nat. Hist.* (Zool.) **3**: 212, pl. 3 fig. a.
B.M. No. 1969.8.26.137.

1 specimen, 280 mm. in S.L. Taken in deep water at the entrance to Tarawa lagoon.

D. XI 16, the fourth spine being the longest. A. III 8, the third spine the longest. Pect. I 16; depth 105 mm.; head 111 mm.; eye 18 mm.; Depth in S.L. 2·6; head in S.L. 2·5; eye in head 6·2; interorbital space 21 mm. Gillrakers on first arch 9+16. Scales ctenoid posteriorly, cycloid anteriorly in front of a line drawn between the origins of the dorsal fin and the pelvic fins.

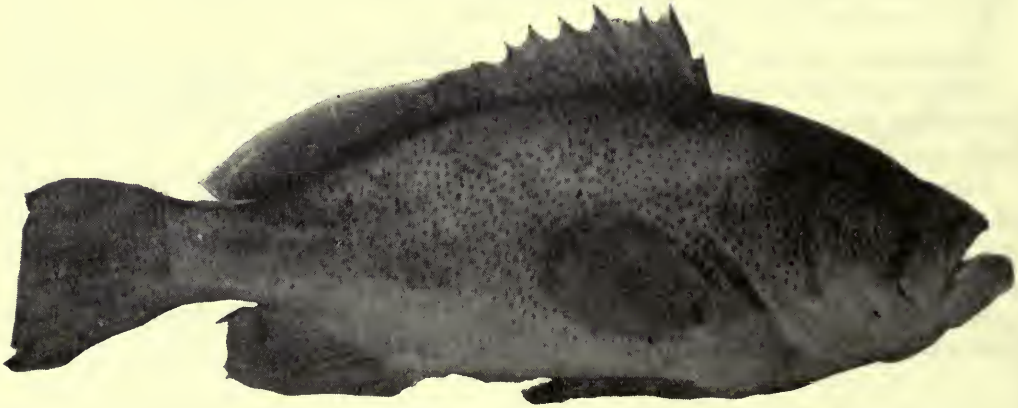

FIG. 2. Photograph of *Epinephelus kohleri*, to show markings.

Live colours pale blue all over, with many brown spots and larger blotches.

This species is apparently quite rare in these waters, but it is known to most of the deep-water fishermen, who fish at night. They say that this species may be poisonous in certain localities, as in the entrance to Tarawa lagoon. This particular specimen is not so deep-bodied as was a previous one seen by Mrs. Cooper, nor had it so many of the larger blotches on the body. Chan (1968) has recently reported this species for the first time from the Macclesfield Bank and Pratas Reef in the South China Sea.

This is a new record for the Gilbert Islands, the species previously being known from Rongarik and Bikini Atolls in the Marshall and Marianas Islands and from New Caledonia.

Epinephelus hexagonatus (Schneider)

Holocentrus hexagonatus Schneider, 1801, *Syst. Ichth. Bloch.*: 323.
B.M. No. 1969.8.26.138–141.

4 specimens, 63–161 mm. in S.L. Taken at Betio, Tarawa in bomb-crater tide pool.

The markings on the two smaller examples tend to be more distinct than in the larger specimens. Gill-raker counts on first arch, including rudiments, are between 24–25. Pectoral rays 18.

Epinephelus merra Bloch

Epinephelus merra Bloch, 1793, *Naturg. ausland. Fische* **7**: Pt. 10: 17.
B.M. No. 1969,8.26.142–144.

3 specimens, 125–153 mm. in S.L. Taken at Betio, Tarawa in bomb-crater tide pool.

Gill-raker counts on first arch, including rudiments, 21–23.

Epinephelus corallicola Val.

Epinephelus corallicola Valenciennes, 1828, *Hist. nat. Poissons* **2**: 336.
Epinephelus macrospilus Bleeker, 1873–1876, *Atlas ichthyol. Indes orient. Neerl.* **7**: 33.
B.M. No. 1969.8.26.145–146.

2 specimens, 132 and 138 mm. in S.L. Taken at Betio, Tarawa in bomb-crater tide pool with the previous two species.

According to Schultz in Schultz et al (1953) these specimens would be *E. macrospilus* (Bleeker), which he considers a valid species. I follow Randall (1955) in this instance and consider *E. macrospilus* to be a synonym of *E. corallicola*.

* ***Epinephelus summana*** (Forsskål)

Perca summana Forsskål, 1775, *Descriptiones Animalium* . . .: xi, 42.
B.M. No. 1969.8.26.147.

1 specimen, 96 mm. in S.L. Taken at Betio, Tarawa in lagoon reef.

D. XI 16; A. III 9; pectoral 16; head 39 mm.; eye 7·5 mm.; interorbital 5 mm.

Live colour light brown, with pale blue-green spots scattered over the body and unpaired fins.

This species does not appear to have been recorded previously from the Gilbert Islands.

Epinephelus sp.

B.M. No. 1969.8.26.148–149.

2 specimens, 39 and 43 mm. in S.L. taken at Betio, Tarawa.

I have not found it possible satisfactorily to assign either of these two juveniles to a definite species.

Cephalopholis argus Schneider

Cephalopholis argus Schneider, 1801, *Syst. Ichth. Bloch.*: 311.
B.M. No. 1969.8.26.150–153.

4 specimens, 70–90 mm. in S.L. Taken at Betio, Tarawa in bomb-crater tide pool.

PSEUDOCHROMIDAE

For the purpose of this paper, I am following Schultz (1953) and Randall (1955) in placing *Plesiops* in the family Pseudochromidae, with the genera *Pseudochromis*, *Pseudogramma* and *Pseudoplesiops*.

Plesiops nigricans (Rüppell)

Pharopteryx nigricans Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 15, pl. 4 fig. 2.
B.M. No. 1969.8.26.154.

1 specimen, 68 mm. in S.L. Taken at Betio, Tarawa in bomb-crater tide pool.

Live colour was a dark brown, with numerous light blue-green spots on the body and unpaired fins.

D. XII 7; A. III 8.

* ***Plesiops melas*** Bleeker

Plesiops melas Bleeker, 1849, *Verh. batav. Genoot.* **22**: 9.
B.M. No. 1969.8.26.155–157.

3 specimens, 30–40 mm. in S.L. Taken at Betio, Tarawa in lagoon reef.

D. X-XI 7–8; A. III 8. This species, which is a new record for the Gilbert Islands, may be distinguished from *P. nigricans* by the lower number of dorsal fin spines and by the lack of an ocellated blackish spot on the operculum.

APOGONIDAE

Apogon novemfasciatus Cuvier

Apogon novemfasciatus Cuvier, 1828, *Hist. nat. Poissons* **2**: 154.
B.M. No. 1969.8.26.158–162.

5 specimens, 38–76 mm. in S.L. Taken at Betio, Tarawa in tide pool.

CARANGIDAE

Alectis ciliaris (Bloch)

Zeus ciliaris Bloch, 1788, *Naturg. ausland. Fische*: 29.
B.M. No. 1969.8.26.163.

1 specimen, 329 mm. in S.L. Taken in Tarawa lagoon, where it was netted.

This appears to be only the second record of this species from the area, the first having been that of Günther (1876), listed as from the Kingsmill Islands. This fish is seen in shoals at infrequent intervals at Tarawa, when it is caught in nets in the lagoon. At the time that the present specimen was taken, several examples had been caught within the space of a few months. This caused great interest amongst the younger Gilbertese, most of whom had never before seen this fish. Live colour was bluish above and plain silvery below, with dorsal and anal fins banded with black and white.

CHAETODONTIDAE

Chaetodon lunula (Lacepède)

Pomacentrus lunula Lacepède, 1802, *Hist. nat. Poissons* **4:** 507.
B.M. No. 1969.8.26.164–166.

3 specimens, 64–91 mm. in S.L. from Tarawa lagoon.

This species has a broad black ocular band extending from the head to the border of the preoperculum. Posterior to this is a pale band. There is a triangular shaped dark band extending from above the pectoral base to the middle of the spinous dorsal, where it is narrowest. There is a large black blotch on the caudal peduncle, narrowing to a thin line as it extends forward along the base of the soft dorsal. In smaller examples there is a black blotch, surrounded by a paler band, at the base of the middle of the soft dorsal.

Chaetodon vagabundus Linnaeus

Chaetodon vagabundus Linnaeus, 1758, *Syst. Nat.* (*Ed.* 10): 276.
B.M. No. 1969.8.26.167–168.

2 specimens, 51 and 81 mm. in S.L. from Tarawa lagoon.

There is an ocular band commencing just forward of the dorsal origin and extending through the eye to the ventral edge of the preoperculum. Dorsally, this is narrower than the eye, ventrally broader than the eye. Dorsal fin with a broad marginal black band, not continued on to the last few rays. There is a broad dark band running along the base of the soft dorsal and extending across the caudal peduncle on to the last few anal rays. Caudal fin with a broad, crescent shaped dark band across the centre of the fin. Posterior to this is a narrow dark submarginal band, with the margin of the fin hyaline. On the body are about 6 thin black lines running obliquely backwards and upwards from behind the head and 10 to 11 similar dark lines running obliquely backwards and downwards towards the anal base.

POMACENTRIDAE

Amphiprion bicinctus Rüppell

Amphiprion bicinctus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 139.
B.M. No. 1969.8.26.169.

1 specimen, 79 mm. in S.L. from Tarawa lagoon.

LABRIDAE

Stethojulis axillaris (Quoy & Gaimard)

Julis axillaris Quoy & Gaimard, 1824, *Voy. de l'Uranie et de la Physicienne Zool.*: 272
B.M. No. 1969. 8.26.170–178.

9 specimens, 49–61 mm. in S.L. from Tarawa lagoon.

This species appears to be quite common throughout Oceania.

Halichoeres marginatus Rüppell

Halichoeres marginatus Rüppell, 1835, *Neue Wirbelth. Fische*: 16.
Julis notopsis Valenciennes, 1839, *in* Cuvier & Valenciennes, *Hist. nat. Poissons* **13**: 485.
B.M. No. 1969.8.26.179–180.

2 specimens, 37 and 42 mm. In S.L. from bomb-crater tide pool at Betio, Tarawa.

The prominent ocellated black spot on the dorsal fin is still very clear in both these young specimens. Both Randall (1955) and Schultz in Schultz et al (1960) consider that *Julis notopsis* Cuvier and Valenciennes represents the juvenile form of this species.

Halichoeres trimaculatus (Quoy & Gaimard)

Julis trimaculata Quoy & Gaimard, 1834, *Voy. "Astrolabe" Zool.* **3**: 705.
B.M. No. 1969.8.26.181–207.

27 specimens, 26–103 mm. in S.L. from bomb-crater tide pool, Betio, Tarawa. Very abundant in this area.

Thalassoma lunare (Linnaeus)

Labrus lunaris Linnaeus, 1758, *Syst. Nat.* (*Ed.* 10): 283.
B.M. No. 1969.8.26.208–211.

4 specimens, 53–63 mm. in S.L. from Tarawa lagoon.

* ***Thalassoma amblycephalus*** (Bleeker)

Julis amblycephalus Bleeker, 1856. *Natuurk. Tijdschr. Ned. Indie* **11**: 83.
B.M. No. 1969.8.26.212.

1 specimen, 30 mm. in S.L. from Tarawa lagoon.

This is the first record for this species from the Gilbert and Ellice Islands, although it is widely distributed throughout the south west Pacific and the Philippines.

The colour pattern in the young of this species is somewhat different from that of the adults, consisting of a black band extending from the snout, through the eye, to the base of the caudal fin, its width being about equal to eye diameter. There is a second black band commencing on the head between the eyes and extending back along the side of the dorsal fin, disappearing about halfway along the base of the soft dorsal fin.

D. VIII 13; A. III 14. Pores in lateral line 19+2+6.

ELEOTRIDAE

Eleotriodes sexguttatus (Valenciennes)

Eleotris sexguttatus Valenciennes, 1837, *Hist. nat. Poissons* **12:** 254.
B.M. No. 1969.8.26.213–214.

2 specimens, 40 and 76 mm. in S.L. from bomb-crater tide pool, Betio, Tarawa.

This species appears to be widely distributed throughout the western South Pacific, the Philippines and the Indian Ocean to Ceylon.

* ***Asterropteryx semipunctatus*** Rüppell

Asterropteryx semipunctatus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 138
B.M. No. 1969.8.26.215.

1 specimen, 23 mm. in S.L., taken at Betio, Tarawa from bomb-crater tide pool on the south reef.

Although widely distributed throughout the west Pacific, Hawaii and in the Indian Ocean, this is the first record of this species from the Gilbert Islands.

D. VI 8; A. I 7. Lateral line scales 24. This specimen has three spines at the angle of the preoperculum and has the second and third rays of the first dorsal prolonged beyond the membrane.

GOBIIDAE

Bathygobius fuscus (Rüppell)

Gobius fuscus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 137.
B.M. No. 1969.8.26.216–222.

7 specimens, 28–53 mm. in S.L. Taken in bomb-crater tide pool at Tarawa.

* ***Acentrogobius cauerensis*** (Bleeker)

Gobius cauerensis Bleeker, 1853. *Natuurk. Tijdschr. Ned. Indie* **4:** 269.
B.M. No. 1969.8.26.223–237.

15 specimens, 29–41 mm. in S.L. Taken from bomb-crater tide pool at Betio, Tarawa.

A new record for the Gilbert and Ellice Islands, although known from a wide area of the Pacific.

D. VI 11; A. I 11. Pect. 16. Lateral line scales 29–30. Cheek and operculum scaled. No free silk-like rays in pectoral fin.

Acentrogobius sp.

B.M. No. 1969.8.26.238–239.

2 specimens, 18 and 20 mm. in S.L. from bomb-crater tide pool, Tarawa.

Callogobius sclateri (Steindachner)

Eleotris sclateri Steindachner, 1880, *Sitz. ber. Akad. Wiss. Wien* **80:** 157.
B.M. No. 1969.8.26.240

1 specimen, 27 mm. in S.L. from tide pool, Betio, Tarawa.

D. VI 1 9; A. I 8; Pect. 16. Lateral line scales ca. 31. Scales are cycloid anteriorly, ctenoid posteriorly. There is a raised row of papillae on the snout, two rows on each cheek and one row transversely behind each eye. There are no free silk-like rays in the pectoral fin and no basal membrane on the pelvic fins.

This species was provisionally recorded from the Gilbert Islands by Randall (1955) as *Mucogobius sclateri*.

* ***Quisquilius eugenius*** Jordan & Evermann

Quisquilius eugenius Jordan & Evermann, 1904, *Bull. U.S. Fish Comm.* **22:** 203.
B.M. No. 1969.8.26.241.

1 specimen, 16 mm. in S.L. from Tarawa lagoon.

Not previously recorded from the Gilbert Islands. Apart from the number of predorsal scales, which appear to be absent in this specimen, this fish agrees in all respects with the description of *Q. eugenius*, as well as with an example sent for comparison by the late Professor J. L. B. Smith.

* ***Quisquilius inhaca*** (Smith)

Gobius inhaca Smith, J. L. B., 1949, *Ann. Mag. nat. Hist.* (12) **2:** 103.
B.M. No. 1969.8.26.242–244.

3 specimens, 19–23 mm. in S.L. from Tarawa lagoon.

D. VI 10; A I 8; pect. 16–17. Lateral line scales 28.

These specimens show the characteristic reticulate appearance of the body caused by the edges of the scales being outlined by a dark line, and by the three to four light vertical bars on the head region. This species has not previously been recorded from the Gilbert Islands, and its range must now be extended from Inhaca, Mozambique to this area.

BLENNIIDAE

Istiblennius edentulus (Schneider)

Blennius edentulus Schneider, 1801, *Syst. Ichth.* Bloch.: 172.
B.M. No. 1969.8.26.245–246.

2 specimens, 56 and 68 mm. in S.L. from a tide pool at Bairiki, Tarawa.

D. XIII 20; A. II 22. Live colour grey and green on the back. Dorsal fin grey-green, with lines of darker spots. Outer edge of fin a brilliant blue-black. Anal fin a pale greenish grey, with two pale blue lines shading to blue-black. Extreme edge of fin a pale blue. Pectoral fins yellowish, pelvics hyaline.

Istiblennius lineatus (Valenciennes)

Salarias lineatus Valenciennes, 1836, *Hist. nat. Poissons* **11**: 314.
B.M. No. 1969.8.26.247.

1 specimen, 99 mm. in S.L. from Tarawa tide pool.

D. XII 22; A. II 24.

Istiblennius paulus (Bryan & Herre)

Salarias paulus Bryan & Herre, 1903, *Occ. Pap. B. P. Bishop Mus.* **2**: 136.
B.M. 1969.8.26.248.–249.

2 specimens, 27 and 40 mm. in S.L. from outer reef, tide pools at Bairiki, Tarawa, where it is quite common.

It is with some hesitation that I include the smaller of these two specimens in this species.

Live colour, upper 2/3 of body pale brown, spotted with red, the lower 1/3 being a pale blue. Six dark brown inverted Y-shaped bars, with two turquoise dots per bar. Head brown with red spots. Preoperculum yellow. First dorsal spotted with red; soft dorsal rays cream, the membrane brown. The first half of this fin is also spotted with red. Anal fin becoming a dusky brown distally. Pectorals hyaline, pelvic fins white.

* *Istiblennius cyanostigma* (Bleeker)

Salarias cyanostigma Bleeker, 1849, *Verh. Batav. Genoots.* **22**: 5.
B.M. No. 1969.8.26.250–254.

5 specimens, 43–58 mm. in S.L. from Tarawa lagoon.

D. XIII 20; A. II 20; pect. 14. A well developed nuchal crest present. Supraorbital cirrus simple. Nasal cirrus multifid. No nuchal cirrus. A well developed, recurved canine present on each side of the lower jaw. No well defined colour pattern evident on any of these specimens. Although fairly widely distributed in the central and south tropical Pacific, this species does not appear to have been recorded previously from the Gilbert Islands.

* ***Petroscirtes mitratus*** Rüppell

Petroscirtes mitratus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 111.
B.M. No. 1969.8.26.255–256.

2 specimens, 17 and 43 mm. in S.L. Taken on the reef edge in the lagoon at Bairiki, Tarawa.

D. 26; A. 17; pect. 14. Origin of dorsal fin between hind edge of eye and preoperculum. Colour in alcohol brownish, with dark blotches or transverse bands on body. Five dark edged ocelli along the dorsal part of the body.

Although widely distributed throughout the Indo-Australian region from the Red Sea, down the coast of East Africa, across the Indian Ocean to the Philippines, Australia and the western South Pacific, this species has not previously been recorded from the Gilbert Islands.

CLINIDAE

Tripterygion minutus Günther

Tripterygium minutum Günther, 1877, *J. Mus. Godeffroy* **4**: Pt 13: 211.
B.M. No. 1969.8.26.257.

1 specimen, 20 mm. in S.L. from tide pool on edge of outer reef, Tarawa.

Live colour stated to have been banded with green and cream.

SCORPAENIDAE

Randall (1955) listed only six species of scorpion fishes from Onotoa. Three of the five species dealt with here represent new records for the area.

Scorpaena albobrunneus Günther

Scorpaena albobrunneus Günther, 1873, *J. Mus. Godeffroy* **2**: Pt 3: 77.
B.M. No. 1969.8.26.258–259.

2 specimens, 44 and 48 mm. in S.L. Taken on the west reef at Betio, Tarawa amongst branches of coral.

Live colours brown, with patches of bright yellowish green. Pectorals yellow.

* ***Scorpaenodes guamensis*** (Quoy & Gaimard)

Scorpaena guamensis Quoy & Gaimard, 1824, *Voy. de l'Uranie et de la Physicienne, Zool.*: 326.
B.M. No. 1969.8.26.260–270.

11 specimens, 39–63 mm. in S.L. from the S.W. outer reef, Betio, Tarawa.

D. XIII 7–8; A III 5; pect. 18. Lateral line pores 24–25.

Live colour a rich mottled brown. Pectoral and caudal fins clear, with bright orange spots.

Although widely distributed throughout the Indo-Australian archipelago and the Philippines, this species has not been recorded before from the Gilbert Islands.

* **Sebastapistes nuchalis** (Günther)

Scorpaena nuchalis Günther, 1874, *J. Mus. Godeffroy* **2–3:** Pts 5–6: 76.
B.M. No. 1969.8.26.271–279.

9 specimens, 17–43 mm. in S.L., from the S.E. reef at Betio, Tarawa.

D. XII 8–9; A. III 5; pect. 15. Lateral line with 22–24 tubular scales. Teeth present on vomer and palatines. Body scales mostly ctenoid.

Not previously recorded from this group of islands. Stated by Smith (1957) to be abundant throughout East African waters and at all the islands beyond to the Seychelles.

There is a further specimen, 38 mm. in S.L. which I include with this species, although it possesses 13 dorsal spines. In all other respects it agrees with the nine other specimens identified as *S. nuchalis* and was taken with them.

Dendrochirus zebra (Quoy & Gaimard)

Pterois zebra Quoy & Gaimard, 1824, *Voy. de l'Uranie et de la Physicienne, Zool.*: 329.
B.M. No. 1969.8.26.280–282.

3 specimens, 65–112 mm. in S.L. from bomb-crater tide pool at Betio, Tarawa.

D. XIII 9; A. III 5. Scale rows above lateral line 48–50. Middorsal spines longer than depth of body.

* **Pterois antennata** (Bloch)

Scorpaena antennata Bloch, 1787, *Naturg. ausländ. Fische* **3:** 21.
B.M. No. 1969.8.26.283–284.

2 specimens, 28 and 70 mm. in S.L. from the S.W. outer reef, Betio, Tarawa.

D. XII 11; A. III 6; pect. 17. Scales above lateral line about 50.

This species is widely distributed throughout the Western Pacific and the Indo-Australian region, although according to Smith (1957), it is nowhere abundant. It has not previously been recorded from the Gilbert Islands.

There are two juveniles, 14 and 15 mm. in S.L., which I am provisionally identifying as this species.

SYNANCEJIDAE

* **Synanceja verrucosa** Schneider

Synanceja verrucosa Schneider, 1801, *Syst. Ichth. Bloch.*: 195.
B.M. No. 1969.8.26.285–287.

3 specimens, 104–165 mm. in S.L., taken from the bomb-crater tide pool at Betio, Tarawa.

D. XIII 7; A. III 6; pect. 18.

Live colour greyish green, the pectorals edged with orange.

Widely distributed throughout the Indian Ocean from the east coast of Africa across to India and Ceylon, through Indonesia, the South China Sea and the Philippines to the western South Pacific, and the Indo-Australian region.

Not previously recorded from the Gilbert Islands, although Randall (1955) stated that it was clear that this species was present in the islands. It may be distinguished by the presence of a deep pit behind each eye, the latter being separated by an elevated bony area. There is also a small, deep groove below each eye.

CARACANTHIDAE

Caracanthus maculatus (Gray)

Micropus maculatus Gray, 1831, *Zool. Misc.*: 20.
B.M. No. 1969.8.26.289.

1 specimen, 42 mm. in S.L., taken on the west reef at Betio, Tarawa, between branches of coral.

D. VII 12 ; A. II 11 ; pect. 14. Live colour grey, with a pink cast. Body covered with black spots.

BOTHIDAE

Bothus mancus (Broussonet)

Pleuronectes mancus Broussonet, 1782, *Ichthyologia*, fig. and text (no pagination.)
B.M. No. 1969.8.26.299–302.

4 specimens, 92–167 mm. in S.L. from Tarawa lagoon.

D. 99; A. 78.

The colouration of this species is somewhat similar to *B. pantherinus*, but the two may be distinguished, as stated by Randall (1955), by the difference in the squamation of the interorbital. In *B. mancus* the anterior part of this area is naked, whereas in *B. pantherinus* it is scaled.

Bothus pantherinus (Rüppell)

Rhombus pantherinus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 121.
B.M. No. 1969.8.26.303–305.

3 specimens, 71–145 mm. in S.L., from Tarawa lagoon.

D. 90; A. 71.

BALISTIDAE

* ***Pseudobalistes flavimarginatus*** (Rüppell)

Balistes flavimarginatus Rüppell, 1828, *Atlas Reise nörd. Afrika. Fische des rothen Meeres*: 33.
B.M. No. 1969.8.26.306–307.

2 specimens, 59 and 390 mm. in S.L., taken in Tarawa lagoon, near the reef.

D. III 2 24; A. 24; pect. 15. Lateral line ca. 35 pored scales.

Live colour of the smaller specimen was orange yellow on the body, with many brown spots; the larger specimen was dark greenish brown on the body, the head being a pale orange except above the eye, where it was brown. Fins darkish basally, with two orange lines separated by a dark line on the distal edge.

Not previously recorded from the Gilbert Islands, although apparently not uncommon in Tarawa lagoon, where it is caught both in nets and on a hook.

ANTENNARIIDAE

Antennarius altipinnis Smith & Radcliffe

Antennarius altipinnis Smith & Radcliffe, 1912, *in* Radcliffe, *Proc. U.S. Nat. Mus.* **42**: 204.

B.M. No. 1969.8.26.308–310.

3 specimens, 28–28 mm. in S.L. Taken from the S.W. outer reef at Betio, Tarawa.

The largest of these three specimens is abnormal in possessing only 9 dorsal rays instead of the usual 12. In all other respects it agrees with the description of *A. altipinnis.*

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My thanks are due to the late Professor J. L. B. Smith for the loan of specimens of *Quisquilius eugenius* and *Q. inhaca*; to Dr. R. J. Lavenberg and the authorities of the Los Angeles Co. Museum for lending me a paratype of *Phaenomonas pinnata*; to Dr. P. H. J. Castle, for information on the Ophichthidae, and to my colleagues in the Fish Section for help and criticism during the preparation of this paper.

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A REVIEW OF THE SOUTH AMERICAN IGUANID LIZARD GENUS *PLICA*

By RICHARD ETHERIDGE

SYNOPSIS

The nomenclatorial history, taxonomy, distribution, and external morphology of the iguanid lizard genus *Plica* are reviewed, and the genus is compared with related iguanid genera. *Plica plica* and *Plica umbra* are recognized as the only valid species. Geographic variation in *Plica umbra* is discussed, and two races are recognized : the nominate form in Venezuela and the Guianas, and *P. u. ochrocollaris* Spix in the Amazonian basin of northern Bolivia, Peru, Ecuador, Colombia, and northern Brazil. Use of the generic name *Uranoscodon* Boie is discussed, and *Lacerta superciliosa* is designated as its type species.

INTRODUCTION

Plica plica and *Plica umbra* are among the most abundant, widespread, and earliest known lizards of South America. Their range includes most of northern South America east of the Andes as far to the south as northern Bolivia, and save for the northern parts of Venezuela and Trinidad, from which *P. umbra* is absent, they are often to be found in the same locale. Both species are conspicuous, arboreal insectivores, and they are exceedingly similar in choice of habitat, diet, movements, and general reactions.

In physical appearance the two species are quite different, and they are easy to distinguish in the field. *Plica plica* has small dorsal and ventral scales, tufts of spines on the sides of the neck, and a colour pattern of dark brown bands or marbling on a background of light to olive green, a white chin with a black throat and a narrow, black collar. *Plica umbra* has large dorsal and ventral scales, no spiny scales on the neck, and a colour pattern that is highly variable as well as metachromatic, consisting basically of wide bands or blotches of red, brown, or yellow on a background in some shade of green. Another curious distinction is the colour of the lining of the mouth : white in *plica*, and deep violet in *umbra*.

The nomenclatorial history of *Plica* and related genera has been long and extremely confused. Two other species are now incorrectly recognized : *P. tuberculatum* Andersson (1918 : 2), and *P. stejnegeri* Burt & Burt (1930 : 24), and two currently recognized species of *Tropidurus*, *T. holotropis* Boulenger (1912 : 420), and *T. unicarinatus* Werner (1899 : 480) are actually synonyms of *Plica umbra*. The genus *Plica* itself has never been adequately characterized or diagnosed, and in mots European museums it is still catalogued under the name *Uraniscodon* Kaup.

In this study the history of the nomenclature of *Plica* is presented, the genus is defined and diagnosed, its species are redescribed and accompanied by synonomies, and geographic variation in *Plica umbra* is discussed.

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The following abbreviations are used :

A.M.N.H.	American Museum of Natural History, New York.
B.M.N.H.	British Museum (Natural History), London.
C.A.S.	California Academy of Sciences, San Francisco.
F.M.N.H.	Field Museum of Natural History, Chicago.
L.A.C.M.	Los Angeles County Museum, Los Angeles.
M.C.Z.	Museum of Comparative Zoology, Harvard University, Cambridge.
M.H.N.P.	Muséum National d'Histoire Naturelle, Paris.
N.M.W.	Naturhistorischen Museum, Wien.
N.R.M.S.	Naturhistoriska Riksmuseet, Stockholm.
S.M.F.	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt a.M.
S.M.N.L.	Staatliches Museum für Naturkunde, Ludwigsburg.
S.N.M.	Stanford Natural History Museum, Stanford.
U.S.N.M.	United States National Museum, Washington.
Z.M.B.	Zoologisches Museum der Humboldt Universität, Berlin.
Z.M.H.	Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg.

HISTORICAL REVIEW

Linnaeus (1758) described the two valid species currently referred to the genus *Plica* as *Lacerta Umbra* (pg. 207) from " Meridionalibus, " and *Lacerta Plica* (pg. 208) from " Indiis. " Although Linnaeus made no reference to it a figure of *plica* had been included by Seba (1734 : 11.65.5), a figure which later formed the basis for Laurenti's (1768 : 48) *Iguana chalcidica* from " Gallaccia. "

Latreille placed *umbra* in the genus *Iguana* (1802a : 263), and *plica* in the genus

Stellio (1802b : 27). Later that same year Daudin (1802) employed the combinations *Agama umbra* and *Agama plica*. However, his characterization of *Agama umbra*, based upon specimens from Cayenne and Surinam, is clearly that of Linnaeus' *Lacerta plica*, while his reference to *Agama plica* is based solely on the authority of Linnaeus. Merrem (1820 : 54), and Wied (1825 : 125) also included these species in *Agama*.

Spix (1825 : 10) described *Lophyrus ochrocollaris* from " in sylvis fluminis Amazonum, " and on the following page described *Lophyrus Panthera* from " sylvis ad pagum Ecgá. " The types of both forms, formerly in the Zoologische Sammlung des Bayerischen Staates, München, were destroyed during World War II. However, it is clear from the descriptions and coloured figures of Spix that *ochrocollaris* was based upon a sombre coloured adult of *Plica umbra*, and *panthera* was based upon a brightly coloured juvenile of *Plica plica*.

At this point the nomenclatorial history of *Plica* becomes confused with that of two unrelated genera, *Enyalius* and *Uranoscodon*. Kaup (1825 : 590) described the genus *Uranoscodon*, based upon Linnaeus' (1758 : 200) *Lacerta superciliosa*, although he included as well both *plica* and *umbra*. Boie (1825 : 1090), in commenting upon Kaup's work, indicated that *Agama catenata* (Wied, 1821 : 247), and *Agama picta* (Wied, 1925 : 125) should be included in the same genus with *superciliosa*, for which he suggested that either his own name *Ophryessa*, or *Uraniscodon* (emended from Kaup's *Uranoscodon*) might be used. Boie specifically excluded *plica* and *umbra* from this genus. In the following year Kaup (1826 : 89) adopting Boie's spelling of *Uraniscodon*, gave a more detailed description of the genus, to which he referred eight species. In addition to *superciliosa*, *plica*, and *umbra* he included *Lophyrus rhombifer* (Spix, 1825 : 9), *Lophyrus margaritaceus* (Spix, 1825 : 10), *Agama picta*, *Agama catenata*, and *Agama hispida* (Spix, 1825 : 12). *L. rhombifer* and *L. margaritaceus* are synonyms of *Agama catenata*, and both *catenata* and *picta* are currently referred to as *Enyalius* (Etheridge, 1969). *Agama hispida* Spix is now regarded as a species of *Tropidurus*. Later that year Boie (1826 : 119), in dealing with most of the same species, placed in the genus *Ophryessa* the species *superciliosa*, *catenata*, *margaritaceus*, *ochrocollaris*, *panthera*, and *auronitens*. As pointed out above, *margaritaceus* is a synonym of *catenata*, *ochrocollaris* a synonym of *umbra*, and *panthera* a synonym of *plica* ; *auronitens*, as recognized by Kaup (1826 : 90) is a synonym of *superciliosa*.

Most of the same species were referred to by Fitzinger (1826 : 48), who recognized Boie's *Ophryessa*, in which he included *superciliosa*, *catenata*, *margaritaceus*, and *umbra*. In the genus *Ecphymotes* Fitzinger placed *plica*, *undulatus*, *pictus*, and *acutirostris*. Kaup (1827 : 612) then proposed the subdivision of *Uraniscodon* into three subgenera : *Uraniscodon*, containing *Agama hispida* ; *Pneustes*, containing *picta*, *umbra*, and *plica* ; and *Ophryessa*, containing *superciliosa*, *catenata*, and *margaritaceus*.

Wagler (1830 : 150) described the genus *Hypsibatus*, including in it the species *plica*, *umbra*, and *picta*. Wiegmann (1835 : 289) replaced *Hypsibatus* with *Hypsilophus*, pointing out that the former was preoccupied by *Hypsibates* Nitzsch (1827 : 150), a genus of birds.[1]

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[1] Under Article 56 (a) of the current edition of the International Code of Zoological Nomenclature *Hypsibatus* Wagler and *Hypsibates* Nitzsch would not now be considered homonyms, but under Article 23 (b) *Hypsibatus* Wagler is to be considered a *nomen oblitum*.

Gray (1827 : 208) described *Lophyrus agamoides*, which he later (Gray, 1831 : 41) recognized as a synonym of *Plica plica*. Gray (1831 : 40) described *Plica* as a subgenus of *Ophyessa* (an emendation of *Ophryessa* Boie), including in the subgenus *brasiliensis*, *picta*, and *plica*. *Brasiliensis* is unrecognizable from its description, but probably is a synonym of *Enyalius catenatus* (Etheridge, 1969 : 244). The characterization of *Ophyessa* (*Plica*) *picta* is clearly that of *Plica umbra*, although Gray lists as its synonyms *Agama picta* Wied, *Lophyrus ochrocollaris* Spix, and *L. panthera* Spix. The characterization of *plica* is that of *Plica plica*, and listed as its synonyms were *Lacerta plica* Linnaeus, *Agama plica* and *Agama umbra* of Daudin, and *Lophyrus agamoides* Gray.

The confusion between Wied's *Agama picta* (= *Enyalius pictus* fide Etheridge, 1969) and *Plica umbra* was continued by Schinz (1833 : pl. 25 ; 1835 : 86) who figured Wied's species of *Enyalius* under the name *Calotes pictus*, and referred to its synonymy *Lophyrus ochrocollaris* and *L. panthera* of Spix.

Duméril & Bibron (1827) used Wagler's name *Hypsibatus* for two species, *H. agamoides*, and a new form, *H. punctatus*, both of which are clearly synonyms of *Plica plica*. In the same work Duméril & Bibron (1837 : 247) proposed the new genus *Uperanodon*, based on *Plica* of Gray in part, and *Hypsibatus* of Wagler in part. Included in *Uperanodon* were *ochrocollorae*, with *Lacerta umbra* listed as its synonym, and *pictum*, with *Lophyrus panthera* as a synonym.

Fitzinger (1843 : 58) included *umbra* and *pictus* in the genus *Hypsibatus*, with *umbra* designated as type of the subgenus *Hypsibatus*, and *pictus* the type of the subgenus *Uperanodon*. On the following page he included *punctatus* (of Duméril & Bibron) and *plica* in the genus *Ptychosaurus*, designating *punctatus* as the type of the subgenus *Ptychosaurus*, and *plica* as the type of the subgenus *Ptychopleura*.

Gray (1845 : 223) referred two species to *Uraniscodon* : *umbra*, based on a specimen from Pernambuco that is clearly *Plica umbra*, and *pictum*, based on Wied's description of *Agama picta*. He then refers to *Plica umbra*, based on a specimen of uncertain locality and referable to *Plica plica*, and *Plica punctata* (p. 224) based on the description of *Hypsibatus punctatus*.

Cope (1876 : 170) described *Hyperanodon peltigerus* from Peru, another synonym of *Plica umbra*.

Boulenger (1885 : 179–180) did a remarkably good job of untangling the confused history of the genus, correctly recognizing the existence of only two valid species, and erring only in the consideration of *Agama picta* as a synonym of *umbra*, and in using the generic name *Uraniscodon* rather than *Plica*.

Stejneger (1901 : 182) pointed out that Kaup's original description of *Uranoscodon* was based upon *Lacerta superciliosa*, although *plica* and *umbra* were included by Kaup in the genus, and that Boie (1825 : 1090) specifically excluded *plica* and *umbra* from the genus. Although this may not be considered a formal designation of the type species of *Uranoscodon*, as Stejneger believed, to do so now would certainly seem to be the desirable course. I therefore designate *Lacerta superciliosa* Linnaeus (1758 : 200) as the type species of the genus *Uranoscodon* Kaup (1825 : 590). Note that although Fitzinger (1843 : 16) designated *superciliosa* as type of the subgenus

Ophryoëssa (emended from *Ophryessa*), Boie did not publish the description of *Ophryessa* until several months after the publication of Kaup's *Uranoscodon.*

Following the appearance of Boulenger's catalogue, three additional names have been proposed for *Plica umbra* : *Tropidurus unicarinatus* from Surinam (Werner, 1899 : 480), *Tropidurus holotropis* from Peru (Boulenger, 1912 : 420), and *Plica tuberculatum* from Bolivia (Andersson, 1918 : 2). An additional new species, described as *Plica stejnegeri* (Burt & Burt, 1930 : 24), is a synonym of *Tropidurus spinulosus.*

A review of the recent literature, and of the catalogues of numerous museums in the United States and Europe indicates that at the present writing *Tropidurus holotropis, T. unicarinatus, Plica tuberculatum,* and *Plica stejnegeri* are all considered valid.

PLICA Gray, 1831

In Cuvier *edit* Griffith, The Animal Kingdom, *9* : 40. Type species : *Lacerta plica* Linnaeus 1758.

Hypsibatus Wagler, 1830 (preoccupied by *Hypisibates* Nitzsch), p. 150. Type species : *Lacerta umbra* Linnaeus.
Hypsilophus Wiegmann, 1835 (replacement name for *Hypsibatus* Wagler), p. 289.
Uperanodon Duméril & Bibron, 1837, p. 247. Type species : *Lophyrus ochrocollaris* Spix.
Pytchopleura Fitzinger, 1843, p. 59. Type species : *Lacerta plica* Linnaeus.
Ptychosaurus Fitzinger, 1843, p. 59. Type species : *Hypsibatus punctatus* Duméril & Bibron.
Hyperanodon Agassiz, 1847 (replacement name for *Uperanodon* Duméril & Bribon), p. 190.

DEFINITION AND DIAGNOSIS. No adequate characterization or diagnosis of the genus *Plica* has been published. Boulenger (1885 : 179), using the name *Uranoscodon,* listed a number of characteristics that the species *umbra* and *plica* have in common, by which, supposedly, they may be distinguished from other iguanids. Most of the characters listed by Boulenger are shared with one or more other iguanid genera. In his key to the genera of iguanid lizards Boulenger (1885 : 4) employed the characteristics of " digits strongly bent at the articulations ; anterior maxillary teeth longest " to distinguish *Uranoscodon* (that is *Plica* in current usage) from *Tropidurus* : " digits straight ; no canine-like teeth. " The digits are bent at their articulations to at least some degree in *Tropidurus* and *Uracentron,* and in some species of *Tropidurus,* e.g. *spinulosus, pictus,* and *bogerti,* the digits are as strongly bent as they are in *Plica.* The enlargement of anterior maxillary teeth is ontogenetic. Even though they are relatively longer in adult *Plica* than in *Tropidurus,* the condition is approached by some species of *Tropidurus.* Although enlarged anterior maxillary teeth and bent digits will not distinguish *Plica* from other iguanid genera, several other characteristics will.

Plica belongs to a group of South American–West Indian iguanids that is distinguished by the presence of a large sternal fontanelle and the absence of femoral pores, the " tropidurines " (Etheridge, 1964 : 629). Within the tropidurines *Plica* is a member of that section in which the interparietal scale is very much larger than the adjacent scales, a group which also includes *Tropidurus, Uracentron, Strobilurus,* and *Uranoscodon.* The characteristics by which *Plica* may be distinguished from *Tropidurus* are as follows :

Plica	*Tropidurus*
1. Orbit bordered below by 5 to 7 subequal suboculars ; no enlarged preocular.	1. Orbit bordered below by a single, wide, elongate subocular that extend to the anterior corner of the orbit, or is preceded by a large preocular.
2. Loreal scales small and numerous ; several rows of loreolabials.	2. Loreal scales large and few ; 1 or 2 rows of loreolabials.
3. No enlarged postmentals or lateral gulars.	3. One or two pairs of enlarged postmentals, and usually a row of enlarged lateral gulars.
4. Nostral in the approximate centre of nasal scale, directed anterolaterally.	4. Nostral in the posterior part of nasal scale, directed posterolaterally.
5. Superciliaries short and broad, forming a sharp crest.	5. Superciliaries long and narrow, not forming a sharp crest.

The characteristics by which *Plica* may be distinguished from *Uranoscodon* are as follows :

Plica	*Uranoscodon*
1. Upper head scales of various sizes ; supraoculars enlarged ; supraorbital semicircles distinct ; scales flat or convex, or a few conical.	1. Upper head scales small, subequal ; supraoculars small ; supraorbital semicircles not distinct ; scales irregularly pyramidal.
2. Interparietal scale much larger than distance between orbits.	2. Interparietal scale about as wide as distance between orbits.
3. Superciliary crest moderately projecting, the last superciliary not enlarged.	3. Superciliary crest strongly projecting, the last superciliary conspicuously enlarged.
4. Tail long and slender, rounded, without a serrate middorsal crest.	4. Tail long and thick, distinctly compressed, with a serrate middorsal crest.

Plica plica (Linnaeus)

Lacerta Plica Linnaeus, 1758, p. 208 (type locality, " Indiis "; here restricted to the vicinity of Paramaribo, Surinam).
Iguana chalcidica Laurenti, 1768, p. 48 (type locality, " Gallaccia ").
Agama umbra Daudin, 1802, p. 375.
Agama plica Daudin, 1802, p. 412.
Stellio plica Latrielle, 1802b, p. 27.
Lophyrus Panthera Spix, 1825, p. 11 (type locality, " sylvis ad pagum Ecgá, " Brazil).
Ecphymotes Plica Fitzinger, 1826, p. 49.
Uraniscodon plica Kaup, 1826, c. 91.
Uraniscodon (*Pneustes*) *plica* Kaup, 1827, c. 610.
Lophyrus (*Ophryesa*) *Agamoides* Gray, 1827, p. 208.
Hypsibatus Plica Wagler, 1830, p. 150.
Ophyessa (*Plica*) *Plica* Gray, 1831, p. 40.
Hypsibatus agamoides Wiegmann, 1834, p. 15.

Hypsibatus punctatus Duméril & Bibron, 1837, p. 258 (type locality, none given).
Hypsilophus plica Wiegmann, 1835, p. 289.
Ptychosaurus (*Ptychosaurus*) *punctatus* Fitzinger, 1843, p. 59.
Ptychosaurus (*Ptychopleura*) *Plica* Fitzinger, 1843, p. 59.
Plica umbra Gray, 1845, p. 223.
Plica punctata Gray, 1845, p. 224.
Hypsibatus punctatus Peters, 1877, p. 408.
Uraniscodon plica Boulenger, 1885, p. 180.
Plica plica Burt and Burt, 1930, p. 19.

HOLOTYPE. N.R.M. No. KaF 1900 : 112. Linnaeus obviously erred in listing India as the origin of the holotype. Although the ranges of both species of *Plica* in South America are vast, geographic variation in *Plica umbra* is sufficient to narrow the origin of the syntypes of that species to the general region of the Guianas. I have elsewhere (Etheridge, 1968 : 51) pointed out that many of the South American species of plants and animals described by Linnaeus were brought to him from Surinam by Carl Gustaf Dahlberg and Daniel Rolander, the latter a student of Linnaeus, and that most of their collections were made in Paramaribo and the nearby countryside. I, therefore, propose the restriction of the type locality of *Plica plica* to the vicinity of Paramaribo, Surinam.

CHARACTERISTICS. Rostral band-like, about four times wider than high. Nasals convex, above and anterior to canthal ridge, separated from rostral and upper labials by two rows of small scales ; nasal opening directed dorsolaterally. Internasals, frontonasals, and prefrontals small, imbricate, irregularly arranged. Supraorbital semicircles moderately distinct anteriorly, scarcely distinct from adjacent parietal scales posteriorly, medially separated by a row of small scales or with one or two scales in contact medially between the orbits. Four to seven large, transversely widened supraoculars, medially separated from supraorbital semicircles by two rows of small scales, laterally separated from superciliaries by several rows of smaller scales. Interparietal much larger than adjacent scales, a third to a fifth as wide as head, separated from supraorbital semicircles by smaller scales, narrowing in front, with a central " eye. " Scales of parietal and upper temporal region small, irregularly arranged, imbricate, and sharply keeled. An elongate, sharply keeled canthal, followed by four or five elongate, keeled superciliaries, in turn followed by two similar scales overlapping in the opposite direction; the canthal and superciliaries together forming a projecting crest. About 15 imbricating scales in loreal region, not markedly distinct from adjacent loreolabials and scales of preocular region. Orbit bordered below by a well defined arc of large scales of more or less equal size, each with a sharp keel near the upper margin ; no enlarged preocular. Loreolabials in several irregular rows, separating nasals, loreals, and suboculars from upper labials. Temporals small, rhomboidal, imbricate, obtusely keeled ; those bordering anterior margin of ear with a laterally projecting spine. Four to six rectangular upper labials. Mental subtriangular. Five or six lower labials similar to upper labials. No enlarged postmental or lateral gulars. Gulars small, imbricate, smooth anteriorly, becoming smaller still and obtusely keeled near the transverse gular fold ; a medial row of very slightly enlarged scales along margin of dewlap.

A row of enlarged scales aligned middorsally extending from occiput to proximal third of tail, forming in adults a low serration on the neck and anterior back. Dorsal nuchals conical, each with a stout central spine, not distinctly imbricate, becoming smaller still on the sides of the neck ; three patches of markedly enlarged, spinose scales on side of neck, one posteroventral to, and another posterodorsal to the ear opening, the third posterior to the anterodorsal patch. Dorsal body scales keeled, imbricate, the keels forming oblique lines that converge toward the midline posteriorly, each keel ending in a short, outward projecting spine ; dorsolateral body scales becoming gradually smaller until they meet the dorsolateral body fold, the latter provided with slightly larger and more distinctly spinose scales ; below the dorsolateral fold scales becoming gradually larger and less strongly keeled, grading into smooth, rhomboidal, imbricate ventrals.

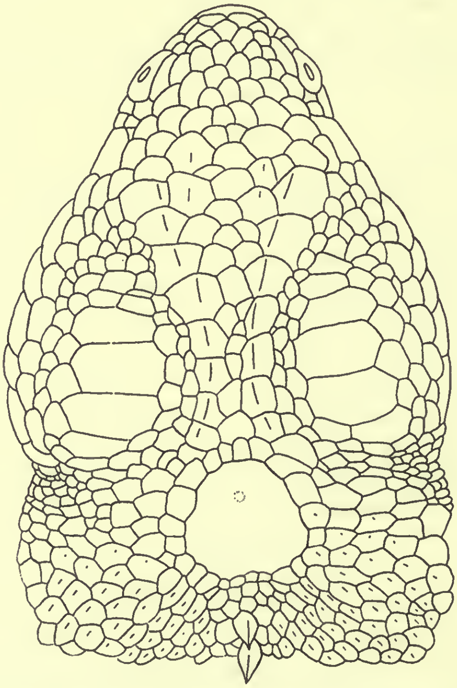

FIG. 1. Dorsal view of the head of *Plica plica* (A.M.N.H. 61315).

Two transverse gular folds, the posterior one rising on each side as an antibrachial fold enclosing granular scales, arching above the forelimb insertion, and continuing back as a dorsolateral body fold to end just above the hindlimb insertion. Sides of neck with strong, irregular folds.

Caudal scales anterior to first autotomy segment similar to body scales above and below ; autotomy annuli distinct, with five scale rows in the first few segments, six rows in segments of the midportion of the tail, and thereafter seven rows in each segment.

Upper limb scales mostly rhomboidal, keeled, imbricate, those of the proximal limb segments also mucronate ; ventral limb scales mostly smooth, imbricate. Supracarpals, supratarsals, and supradigitals keeled, imbricate ; infracarpals and infratarsals each with a median keel ending in a stout spine. Infradigital lamellae each with a sharp, median keel ending in a stout spine, flanked on each side by a much weaker keel and spine. Proximal lamellae of first and second fingers, and first, second and third toes somewhat enlarged dorsoventrally.

COLOUR. The pattern is basically one of cross bands or bold, irregular blotches of black, dark brown, or grey on a background of some shade of green. The anterior cross band usually forms a distinct, very dark collar. Upper surfaces of the limbs are similarly patterned. Small individuals are whitish below ; adult males have a black throat narrowly bordered with yellow, shading into orange that covers the rest of the ventral surfaces of the body, limbs and tail. In life the epithelial lining of the mouth is white. A detailed description of the colour in life of an individual from Kartabo, British Guiana may be found in Beebe (1944 : 204–205). The pattern usually remains distinct even after many years in preservative, with only the background fading to bluish or olive grey.

GEOGRAPHIC VARIATION. Unfortunately the poor state of preservation of most of the specimens examined does not permit a useful analysis of geographic variation in *Plica plica*. The most deviant sample I have seen is from Puerto Ayachuco on the Orinoco River, between Venezuela and Colombia. Specimens from this locality differ from others in having a more acuminate snout, larger dorsal snout scales, slightly smaller dorsal body scales, less well developed lateral neck spines, and a less densely spotted throat in males. Specimens from the vicinity of Esmeralda, Venezuela also have large dorsal snout scales but are otherwise typical. Specimens from northern Venezuela, Trinidad, and the Guianas appear to reach the greatest maximum size, and because of greater development of scale mucrons have overall a more spiny appearance.

RANGE. (Text-fig. 2.) Trinidad and northern South America east of the Andes, including northern Brazil, British Guiana, Surinam, Cayenne, northern Bolivia, eastern Peru, eastern Ecuador, eastern Colombia, and Venezuela except in the northwest.

MATERIAL EXAMINED. *British Guiana* : Kartabo A.M.N.H. 14117, 21331, 21290 ; Kamakuska A.M.N.H. 25071, 25113–5, 25089 ; Kamaria Landing, Cuyuni River A.M.N.H. 8090 ; Groets Creek, Essequibo River A.M.N.H. 8091 ; Kuyuwini Landing A.M.N.H. 61316 ; 30 mi. from Bartica M.C.Z. 81189. *Surinam* : Pomeroon River, Pickersgill M.C.Z. 32492 ; Orleane Kreek M.C.Z. 66887 ; Zanderij B.M.N.H. 1946.4.3.43 ; Paramaribo Z.M.H. 3548 ; no specific locality S.M.F. 11198, M.H.N.P. 2385. *Trinidad* : Tucker Valley A.M.N.H. 64461, 64529 ; Guayaguayase A.M.N.H. 70999 ; hts. of Guanape A.M.N.H. 72808 ; Caura Valley A.M.N.H. 72813–5 ; Mayaro A.M.N.H. 72816 ; Port of Spain, St. Ann's Valley M.C.Z. 9001–3 ; Salibea

Beach M.C.Z. 12064 ; Nariva Swamp at Cascadoux Trace M.C.Z. 60825 ; near Maracas Valley M.C.Z. 60826 ; no specific locality M.C.Z. 79829, 6102, S.M.F. 11200, B.M.N.H. 66.6.16.11–12. *Venezuela* : 6 mi. N. Esmeralda, Mt. Duida region A.M.N.H. 36661–62 ; Raudal de Atures, 10 km S. Puerto Ayachucho A.M.N.H. 81813–4 ; Serro de Cucuchy, La Varre A.M.N.H. 36530–1 ; Rio Pescada A.M.N.H. 36638 ; Mt. Duida A.M.N.H. 36640, M.C.Z. 101841 ; 10 mi. N. Esmeralda A.M.N.H. 36658–9 ; 6 mi. N. Esmeralda A.M.N.H. 36650 ; Estado Bolivar, Bajo Cuchivero, Piedra Pintada C.A.S. 94658 ; Territorio Federal Amazonas, Alto Ventuari, Cacori C.A.S. 94659 ; Paria Peninsula, Yacua M.C.Z. 43861–5 ; Puerto Ayacucho M.C.Z. 58335–6, U.S.N.M. 80629–31, F.M.N.H. 177924–36 ; nr. Rio San Juan, Los Mangos, nr. Caripito M.C.Z. 81185 ; Chacaracual, Estado Sucre M.C.Z. 81186–8 ; Puerto La Cruz U.S.N.M. 121184 ; Brazo Casiquiare U.S.N.M. 83612 ; Cerro Ya-pacana U.S.N.M. 83943 ; Iguapo, Alto Orinoco S.M.F. 11201, M.C.Z. 101837, 101840. *Colombia* : Lower Rio Guayabero, Cerro de las Pinturas F.M.N.H. 165207 ; Comisaria Vaupes, Cano " Agua Bonita," 8 km S.W. San José F.M.N.H. 75691. *Peru* :

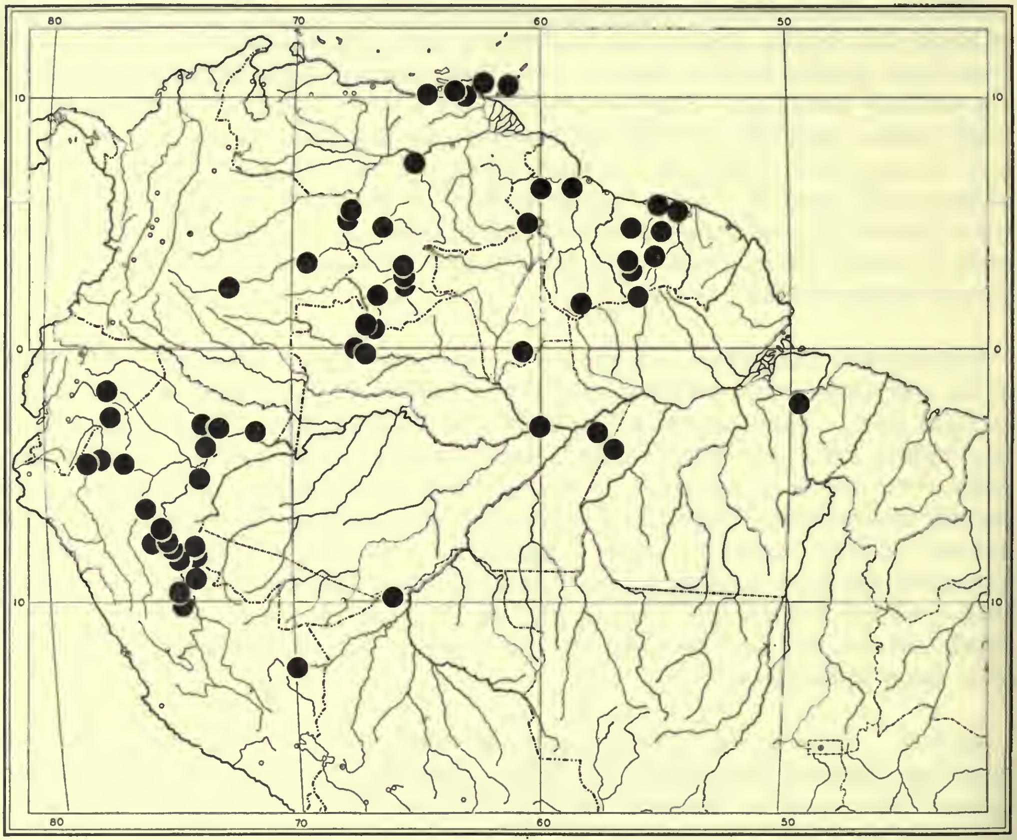

FIG. 2. Map of northern South America showing localities for *Plica plica*.

Utoquina region, Peru–Brazil border A.M.N.H. 56458 ; Monte Alegre, Rio Pachitea system A.M.N.H. 56463 ; east of Contamana on trail to Contaya A.M.N.H. 56463 ; Barranca, Rio Marañon Valley A.M.N.H. 56465 ; Rio Tapiche, trib. of Rio Ucayali A.M.N.H. 56470 ; Rio Panaya mouth, middle of Rio Cushabatay Valley A.M.N.H. 56481, 56483 ; Pan de Azucar, 39 km NNE of Oxapampa, Rio Izcozazin L.A.C.M. 49139 ; Roaboya, Rio Ucayali Valley A.M.N.H. 56441–2, 56471 ; Colonia Calleria, Rio Calleria, 15 km from Ucayali C.A.S. 93243–5 ; mouth of Rio Santiago M.V.Z. 16899 A.M.N.H. 56448, 56462 ; Pebas S.M.N.H. 15142, 12469, A.M.N.H. 8731–2, B.M.N.H. 67.9.17.5 ; Boca de Amigo, Madre de Dios F.M.N.H. 81451–2 ; Rio Samiria, Sta. Elena, Nanta F.M.N.H. 109821 ; Rio Morona, Quebrada Pushaga F.M.N.H. 109826 ; Iquitos F.M.N.H. 45492–5, N.M.W. 13902, A.M.N.H. 56437 ; Yarinacocha, Rio Ucayali F.M.N.H. 56011–20 ; Boca de Rio Inambari, Madre de Dios F.M.N.H. 83305 ; Cayaria B.M.N.H. 81.5.13.23–4 ; lower Cushabatay A.M.N.H. 56431, 56434 ; Rio Tamaya A.M.N.H. 56433, 56473 ; Pilluana, Rio Mishqulyacu A.M.N.H. 56435 ; Rio Ayendama, trib. of Rio Cenipa, Marañon system A.M.N.H. 56438, 56443 ; Rio Itaya, near Iquitos A.M.N.H. 56444, 56484 ; Pampa Hermosa, near mouth of Rio Cushabatay A.M.N.H. 56445–7, 56451–4, 56456, 56460, 56466–9, 56472, 56474–7, 56480, 56488, 56485–6 ; mouth of Rio Napo, Lago Mirano region A.M.N.H. 56449–50 ; Achinamisa, Rio Huallaga system A.M.N.H. 56436, 56457. *Ecuador* : Sarayacu Z.M.B. 9984 ; Rio Pastaza M.C.Z. 37268 ; Santiago, between Rio Santiago and Rio Pastaza, S. of Macas and N. of Gualaquiza F.M.N.H. 42502–4 ; Palatanga B.M.N.H. 80.12.8.55. *Brazil* : Rio Manjuru A.M.N.H. 101938–40, 101942–3 ; Maués A.M.N.H. 101941, 101944 ; Cairari Uaupes, Tatu, on Rio Negro A.M.N.H. 36626 ; Rio Madeira, Abuna C.A.S. 49782 ; Pará, no specific locality M.C.Z. 2890 ; mouth of Rio Canabury U.S.N.M. 83535 ; São Gabriel, Rio Negro U.S.N.M. 83579–81 ; Salto do Huá, on Venezuelan border U.S.N.M. 83566 ; Serro do Cucuhy A.M.N.H. 36530–1 ; Tabatinga F.M.N.H. 83595 ; Cametá, Rio Tocantins N.M.W. 13901 ; Boco do Rio Tucano, Roraime M.C.Z. 87289–90 ; Reserva Ducke, Manaus M.C.Z. 92750 ; no specific locality S.M.F. 11199. *No specific locality* ; M.H.N.P. 2387 (holotype *Hypsibatus punctatus*).

Plica umbra (Linnaeus)

Lacerta Umbra Linnaeus, 1758, p. 207 (type locality, " Meridionalibus " ; here restricted to the vicinity of Paramaribo, Surinam).
Iguana umbra Latreille, 1802a, 263.
Agama umbra Merrem, 1820, p. 54.
Lophyrus ochrócollaris Spix, 1825, p. 10 (type locality, " sylvis fluminis Amazonum, " Brazil).
Ophryessa Umbra Fitzinger, 1826, p. 48.
Uraniscodon Umbra Kaup, 1826, c. 91.
Uraniscodon (*Pneustes*) *umbra* Kaup, 1827, c. 612.
Hypsibatus umbra Wagler, 1830, p. 150.
Uperanodon ochrocollare Duméril & Bibron, 1837, p. 247.
Hypsibatus (*Hypsibatus*) *Umbra* Fitzinger, 1843, p. 58.
Uraniscodon umbra Gray, 1845, p. 223.
Hyperanodon peltigerus Cope, 1876, p. 170 (type locality, Peru).
Hyperanodon umbra Peters, 1877, p. 408.

Hyperanodon panthera Peters, 1877, p. 408.
Uraniscodon umbra Boulenger, 1885, p. 179.
Tropidurus unicarinatus Werner, 1899, p. 602 (type locality, Surinam).
Tropidurus holotropis Boulenger, 1912, p. 420 (type locality, Alpayaca, Rio Pastaza, Ecuador).
Plica tuberculatum Andersson, 1918, p. 2 (type locality, San Fermin, Bolivia).
Plica umbra Burt & Burt, 1930, p. 24.

SYNTYPES. N.R.M. No. 1900 : 111 (2 exs). The syntypes exhibit those characteristics of scalation that are typical of individuals from the region of the Guianas (see discussion of geographic variation below). The reasons applied to the restriction of the type locality of *Plica plica* are equally applicable to this species, and I therefore propose the restriction of the type locality of *Plica umbra* to the vicinity of Paramaribo, Surinam.

CHARACTERISTICS. Rostral strap-like or subtriangular. Nasals moderately large, convex, above and anterior to canthal ridge, separated from rostral and anterior upper labials by one or two small scales ; nasal opening directed dorsolaterally. Scales of internasal, frontonasal, and prefrontal region moderately large, more or less symmetrically arranged. Supraorbital semicircle scales large, usually three pairs in broad contact medially between the orbits. A row of large, transversely widened supraoculars, usually four in number, medially separated from supraorbital semicircles by two rows of small scales, laterally separated from superciliaries by two rows of smaller scales anteriorly ; posterior enlarged supraocular in broad contact laterally with posterior superciliary. Interparietal scale large, a third to half as wide as head, narrowing anteriorly, in broad contact with posterior scales of supraorbital semicircles, with a central " eye." Posterior parietals bordering interparietal small to large, slightly to very strongly convex. A single, elongate canthal, followed by four or five elongate, overlapping superciliaries, in turn followed by three superciliaries overlapping in the opposite direction, the last much the longest ; canthal and superciliaries together form a continuous, projecting crest. Scales of loreal region small, juxtaposed, scarcely distinct from loreolabials or scales of preocular region. Orbit bordered below by an ill defined arc of slightly enlarged, strongly keeled scales of nearly equal size. Loreolabials in several irregular rows, separating loreals and suboculars from upper labials. Temporals small, subimbricate, weakly and obtusely keeled, those bordering the ear anteriorly scarcely projecting. Upper labials four or five, more or less rectangular. Mental subtriangular. Lower labials five or six, similar to upper labials. No enlarged postmentals or enlarged lateral gulars. Gulars small, imbricate, becoming a little smaller, feebly keeled, and bluntly mucronate posteriorly as they approach the transverse gular fold.

A row of scales aligned middorsally beginning at the occiput and extending to the lumbar region, or past the sacral region and onto the tail ; middorsal scales of neck and anterior body distinctly enlarged, forming a denticulate crest. Dorsal scales of body and neck rhomboidal, imbricate, with a blunt posterior keel and a short, blunt mucrone, the keels forming oblique rows that converge toward the midline posteriorly. Lateral neck scales, except those within skin folds, smaller, but otherwise similar to dorsal neck scales ; lateral body scales similar to dorsals, grading into distinctly keeled and mucronate ventrals. Dorsal, lateral and ventral body scales about equal in size, save the anterior laterals which are a trifle smaller.

Strong antibrachial folds containing granular scales, terminating dorsally about halfway between forelimb insertion and median crest, and joining a very strong transverse gular fold ventrally. No lateral body folds and no other lateral neck folds other than antibrachial and gular ; no patches of enlarged scales on sides of neck.

Caudal scales anterior to first autotomy annulus similar to body scales both above and below ; median crest disappears before first autotomy annulus. Autotomy annuli distinct, four scale rows in the first few annuli, five in those of the midportion of the tail, and thereafter six rows. Males lack enlarged postanal scales.

Forelimb scales equal to or a little smaller than body scales, imbricate and keeled, except for proximal postbrachials which are smooth, the keels forming lines more or less parallel to long axis of limb ; postantibrachials more sharply keeled and more strongly mucronate than other forelimb scales. In males, a patch of smooth posterior infrafemorals three or four scale rows wide and about 20 scale rows long ; all other hindlimb scales (as well as all posterior infrafemorals in females) keeled, imbricate, a little larger to a little smaller than body scales. Infracarpals and infratarsals each with a single, stout mucrone. Supradigitals unicarinate ; subdigital lamellae with a strong median keel and mucrone flanked on each side by a much weaker keel and mucrone.

Scale counts are given in Table I. Maximum snout–vent lengths and body–tail proportions of both sexes are given in Table II.

COLOUR. The colour is highly metachromatic, and the pattern exceedingly variable. The pattern is basically one of wide, dark cross-bands or blotches on the body, limbs, and tail, light coloured on the throat and belly, with or without streaks of darker colour, and very dark colour within the antihumeral fold. The background is usually some shade of green, ranging from yellowish-green, to bright green, bluish-green, olive, or olive brown ; the bands and blotches are usually some shade of brown. yellowish-brown, black, red, or orange. In adult males the centre of the throat may be orange, and there is a patch of yellowish colour anterior to the vent and on the lower surface of each femur. In life the epithelial lining of the mouth is deep violet. Beebe (1944 : 207–8) has provided us with a most excellent and detailed description of the colour and pattern of four living animals at Kartabo, British Guiana, and Spix's (1825 : pl. 12, fig. 2) illustration of *Lophyrus ochrocollaris* is a good representation of an adult. In preservative specimens usually become dark purplish brown with still darker markings, although the paler markings of the head and neck frequently persist.

GEOGRAPHIC VARIATION. The very great majority of specimens may be readily identified as one of two distinct types. One of them occurs in the Guianas, the other in the Amazonian Basin of Brazil, Colombia, Ecuador, Peru, Bolivia, and in southern Venezuela. Specimens from intermediate localities are unavailable so that the question of whether two subspecies or two distinct species are involved cannot be resolved with certainty. Tentatively, however, the two forms may be considered subspecies. The syntypes of *Plica umbra* are of the form that occurs in the Guianas. The oldest name available for the Amazonian form appears to be *Lophyrus ochrocollaris* Spix.

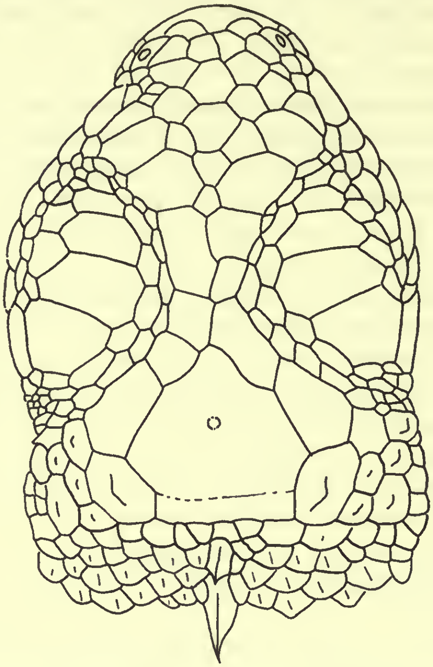

Fig. 3. Dorsal view of the head of *Plica umbra ochrocollaris* (L.A.C.M. 49140).

The two forms may be compared as follows:

ochrocollaris	*umbra*
1. Vertebral scale row prominent from occiput to base of tail, forming a distinct denticulation on the neck.	1. Vertebral scale row prominent on neck and anterior body, becoming indistinguishable from adjacent scales on posterior back, and forming only a slight denticulation on the neck.
2. Dorsal head scales swollen, with blunt, irregular surface.	2. Dorsal head scales smooth or nearly so.
3. A pair of large, distinctly pyramidal scales flank the posterolateral corners of the interparietal.	3. Scales flanking posterolateral corners of interparietal smaller, and flat or nearly so.
4. All scales of body and limbs more sharply keeled and distinctly mucronate.	4. Scales of body and limbs less sharply keeled, less distinctly mucronate, those of the belly only feebly keeled.
5. Scales larger (Table I).	5. Scales smaller (Table I).

Synonyms of *Plica umbra ochrocollaris* are *Hyperanodon peltigerus* Cope, *Tropidurus holotropis* Boulenger, and *Plica tuberculatum* Andersson. A synonym of *Plica umbra umbra* is *Tropidurus unicarinatus* Werner. These synonyms are further discussed in the following section.

REMARKS. Boulenger (1885 : 179–180) adequately dealt with the synonomies of names proposed for *Plica umbra* prior to the appearance of his Catalogue. Subsequently two species of *Tropidurus* have been proposed that are in fact also synonyms of *Plica umbra* : *Tropidurus unicarinatus* (Werner, 1899 : 480), and *Tropidurus holotropis* (Boulenger, 1912 : 420). In their type descriptions both species were compared only with other forms of *Tropidurus*, with no mention of the genus *Plica*. The reasons for their generic allocations were unspecified ; however, the authors apparently based their decision to place these species in *Tropidurus* upon the presence of a very large interparietal scale. In my studies at a large number of American and European museums I was unable to find any specimens, other than the syntypes, catalogued as *Tropidurus unicarinatus*. However, many Ecuadorian and Peruvian specimens of *Plica umbra* are catalogued as *Tropidurus holotropis*, and that name has appeared in such recent faunal lists as Mertens (1956 : 120), and Peters (1967 : 35).

Tropidurus unicarinatus was based upon a subadult female and a male (N.M.V. 18728–9) from Surinam. Both syntypes are in good condition, and are identical in all details of scalation, colour pattern, and proportions with specimens of *Plica umbra* of comparable size from northeastern South America. The number of scales in the vertebral crest from occiput to the anterior margin of the thigh (53, 56), the number of paravertebral scales in the same length (74, 78) and the number of scales around the middle of the body (59, 59) are within the limits of variation for specimens from this region (Table 1).

TABLE 1

Subspecies	Sex	N	Vertebral	Paravertebral	Midbody
umbra	M	19	49–(54·6)–61	70–(78·0)–90	49–(57·1)–71
	F	23	46–(54·7)–63	66–(74·8)–91	48–(56·3)–65
ochrocollaris	M	26	32–(39·8)–46	47–(58·5)–69	43–(49·6)–57
	F	17	36–(40·6)–47	48–(57·2)–67	41–(50·3)–55

Scale counts of the subspecies of *Plica umbra*. N = number of specimens examined for these counts. Vertebral scales are counted along the midline from occiput to a line even with the anterior margin of the thighs held at right angles to the body axis; paravertebral scales are counted for the same distance ; midbody scales are counted around the body midway between the limb insertions. Mean figures are in parentheses.

Tropidurus holotropis was based upon a subadult individual from Alpayaca, Rio Pastaza, Ecuador (B.M.N.H. 1912.11.1.29 [RR 1946.8.29.64]). It is identical in all details of colour pattern, scalation, and proportions with specimens of *Plica umbra* of comparable size from eastern Ecuador. The number of scales in the vertebral crest (35), the paravertebral scale row (55), and around the middle of the body (45) are within the range of variation for specimens from this region (Table 2).

TABLE 2

Subspecies	Sex	N	Snouth–vent Length Range in mm.	Tail/Snouth–vent Length
umbra	M	15	72–100	2·02–(2.24)–2·44
	F	14	61– 94	2·02–(2.18)–2·42
ochrocollaris	M	23	67– 90	2·00–(2.16)–2·51
	F	18	42– 90	1·90–(2.06)–2·33

Snout–vent lengths and tail/snout–vent length ratios for *Plica umbra*.
N = number of specimens examined. Mean figures are in parentheses.

Andersson (1918 : 2) described *Uraniscodon tuberculatum* from San Fermin, northwestern Bolivia, and subsequently Burt and Burt (1930 : 19) referred to the species as *Plica tuberculatum*. Andersson compared *tuberculatum* with *umbra*, from which it was said to differ in the lepidosis of the head, especially the wider interparietal scale, the absence of a feeble, longitudinal fold on the chin, a more strongly raised supracilliary ridge, and a different colour, especially on the head. The holotype (N.R.M. 3256) is a juvenile, 55 mm in snout–vent length, in fair condition except that the skin of the lateral neck region is badly lacerated. Andersson apparently compared the holotype of *tuberculatum* with adult specimens of *Plica umbra* from the northeastern portion of its range, for the differences he noted are clearly due to ontogenetic differences between juveniles and adults, and to geographic variation within the species. The feeble longitudinal fold on the throat of adults is not apparent in juveniles, and the vivid head pattern of juveniles becomes obscure in adults. Although not specifically mentioned by Andersson as a diagnostic character, the large interparietal scale, " much broader than half the breadth of the head," was used by Burt and Burt (1930 : 19) to distinguish *tuberculatum* from *umbra*, " . . . about half as wide as the head." The head width of the holotype is 11·0 mm, the interparietal width 6·4 mm ; thus the interparietal is only slightly more than half (·58) as wide as the head, and within the range of variation of *umbra*. The strongly projecting supracilliary ridge is characteristic of specimens of *umbra* from the western portion of its range. In these, and in all other details of scalation, colour pattern, and body proportions the holotype of *Uraniscodon tuberculatum* is typical of juvenile specimens of *Plica umbra* from the western portion of its range.

RANGE. (Text-fig. 4.) Most of northern South America east of the Andes, including British Guiana, Surinam, Cayenne, southern Venezuela, eastern Colombia, eastern Ecuador, eastern Peru, extreme northern Bolivia, and northern Brazil. The race *P. u. umbra* is confined to the Guianas ; the remainder of the range of the species is occupied by *P. u. ochrocollaris*.

MATERIALS EXAMINED. *Plica umbra umbra*. *British Guiana* : Kartabo A.M.N.H. 21316, 14115–6 ; Kalacoon A.M.N.H. 8097 ; Kamakuska A.M.N.H. 25118 ; Georgetown A.M.N.H. 17690–1 ; Demeara A.M.N.H. 18200, B.M.N.H. 72.10.16.66–7;

Maccasseema B.M.N.H. 87.1.22.7 ; Moraballi Creek, Essequibo River B.M.N.H. 1930.10.10.67–80 ; Mazaruni, Penal settlement B.M.N.H. 1934.11.1.80 ; near Bartica, upper Cuyuni River B.M.N.H. 1934.11.1.79 ; New River B.M.N.H. 1939.1.1.72–3 ; no specific locality A.M.N.H. 61276–8, 61291. *Cayenne* : La Mana M.H.N.P. 2584 ; no specific locality M.H.N.P. 2581, 6828. *Surinam* : Paramaribo Z.M.H. 2229 (2 exs), N.M.W. 13898 (4 exs), 13897 (2 exs), B.M.N.H. xxiii.110.6 ; near Saramaca River, 91·5 kms, B.M.N.H. 1946.4.3.42 ; no specific locality N.M.W. 13899 (5 exs), 18754, 18728–9 (syntypes, *Tropidurus unicarinatus*), S.M.F. 11195.

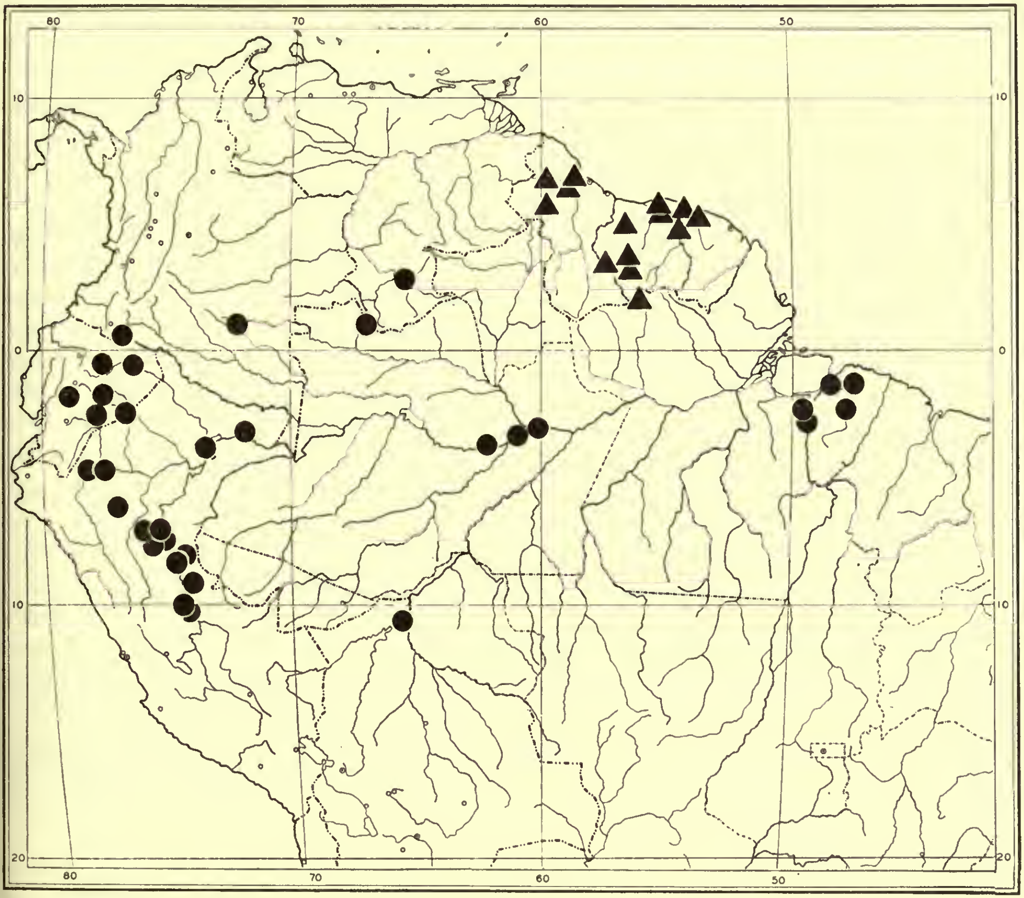

FIG. 4. Map of northern South America showing localities for *Plica umbra umbra* (triangles), and *Plica umbra ochrocollaris* (circles).

No Specific Locality : N.R.M. 1900 (2 exs) (syntypes, *Lacerta umbra*). Additional records from Surinam have been provided to me (*in litt.*) by Mr. Marinus S. Hoogmoed : Wilhelminagebergte, Fallawatra-Coppename, Matta, Cultuurtuin, Coeroenieiland, Sipaliwini, Surinamerivier Powakka, Maguire, Moengo Tapoe, Wanekreek, Djaikreek, Calibi, Tibiti, Kaborkreek, Marowýne Nassaugebergte, Kaiserberg airstrip, Bigiston dist. Marowýne, Boven Nicherie.

Plica umbra ochrocollaris. Ecuador : Montalbo, Rio Bobonaza A.M.N.H. 60607 ; San José de Sumaco A.M.N.H. 28877, 28893 ; Riobamba A.M.N.H. 14573, 23331, M.C.Z. 29291 ; Sarayacu B.M.N.H. 80.12.8.60 ; Rio Pastaza, Alpayaca B.M.N.H. 1912.11.1.29 [RR 1946.8.29.64] (holotype, *Tropidurus holotropis*) ; Santiago, between Macas and Gualaguiza F.M.N.H. 42511 ; Avila, Rio Napo. Prov. Orienta S.N.M. 8269 ; Rio Pastaza M.C.Z. 37269 ; Limon Cocha, Napo M.C.Z. 86685. *Colombia :* Santa Rosa de los Cofanes, Rio Guamués, W. of Puerto Asís F.M.N.H. 165209–10 ; Caquetà, Rio Mecaya F.M.N.H. 69671 ; Puerto Nariño M.C.Z. 61151. *Venezuela :* Esmeralda M.C.Z. 101748 ; La Culebra, upper Rio Cunucunuma M.C.Z. 101749. *Peru* : Rio Pisqui, trib. of Rio Ucayali A.M.N.H. 57183 ; Rio Tamaya, trib. of Rio Ucayali A.M.N.H. 57184 ; Rio Utoquinia, Tapoche region A.M.N.H. 57185 ; Rio Itaya, Iquitos region A.M.N.H. 57186, 57188, 57192, 57197 ; lower Rio Cushabatay, trib. of Rio Ucayali A.M.N.H. 57187 ; Rio Cenipa, trib. of Rio Marañon A.M.N.H. 57184, 57194, 57196 ; Rio Ayendama, trib. of Rio Cenipa A.M.N.H. 57190 ; upper Rio Cushabatay A.M.N.H. 57191 ; Rian Rian, Rio Suhua, Contamana region A.M.N.H. 57193 ; mouth of Rio Santiago A.M.N.H. 57195 ; Guache, Rio Pastaza, at Ecuadorian border A.M.N.H. 60577 ; Moyobamba B.M.N.H. 74.8.4.90–94 ; Iquitos F.M.N.H. 45498 ; Yarinacocha, Rio Ucayali F.M.N.H. 56010 ; Cerro Azul, Dept. Loreto F.M.N.H. 56008 ; Pedrera, Dept. Loreto F.M.N.H. 45497 ; Puerto Mayo F.M.N.H. 3672 ; Pucalpa F.M.N.H. 56009 ; Colonia Calleria, Rio Calleria, 15 km from Rio Ucayali C.A.S. 93241–2 ; Pebas, S.N.M. 8356, 15142, M.C.Z. 16360 ; Pan de Azucar, 39 km NNE Oxapampa L.A.C.M. 49140–2. *Bolivia* : Guayaramerin A.M.N.H. 91857 ; San Fermin N.R.M.S. 3256 (holotype, *Uraniscodon tuberculatum*). *Brazil* : Manaos A.M.N.H. 64859 ; Manacapurú, Rio Solimões A.M.N.H. 4484 (4 exs) S.M.F. 11196–7 ; Cahabouca, Rio Solimões, Paraná do Jacare Z.M.B. 36945 ; Rio Tanantins, upper Amazonas Z.M.B. 30975 (2 exs) ; Rio Capim, SE of Belem Z.S.B.S. 76/1929 ; Piexe-boi, on Braganca road, east of Belem Z.S.B.S. 151/1911 (4 exs) ; Faro Yamundá Z.S.B.S. 91/1960 ; Col. de Vrado Obidon Z.S.B.S. 92/1960 ; Auawindena Z.S.B.S. 93/1960 ; below Torarritius Z.S.B.S. 94/1960 ; Baião, Rio Tocantins, S.W. of Belem N.M.W. 13904 (2 exs) ; Cameta, Rio Tocantins N.M.W. 18179 (2 exs) ; Belem U.S.N.M. 159184–93, M.C.Z. 86685 ; Salto do Huá, on Venezuelan border U.S.N.M. 83567 ; Tabatinga F.M.N.H. 83596–7 ; Codajas, Amazonas B.M.N.H. 1965.1315 ; Rio Guamá, Pará B.M.N.H. 1926.5.5.6 ; no specific locality M.H.N.P. 2383 (2 exs), B.M.N.H. 1961.1083, 53.2.4.106.

Species Erroneously Referred to *Plica*

Burt and Burt (1930 : 19) described *Plica stejnegeri*, based upon a specimen (U.S.N.M. 73505) from " Argentina." Their reasons for referring this species to *Plica* were not specified ; however, they were probably led to this allocation because the skin of the neck is strongly plicate and pouched, and on the sides provided with many tufts of small, erect, spinose scales, a condition that closely resembles that of *Plica plica*.

I have compared the holotype of *Plica stejnegeri*, an adult male, with series of *Tropidurus spinulosus* from Brazil, Bolivia, and Argentina, and find that it is identical in all important details of scalation, colour pattern, and proportions. In this species the scales of the middorsal crest become elongate, two to four times higher than long, in large adults, and the spininess of the body scales, especially those of the lateral neck region and the posterior tibials, becomes more pronounced. *Plica stejnegeri* is thus clearly a synonym of *Tropidurus spinulosus.*

In a recent check list of the lizards of Venezuela Donoso-Barros (1968 : 114) placed *Tropidurus bogerti* Roze (1958 : 247) in the genus *Plica* without comment. Roze discussed in detail the superficial resemblance of *bogerti* to *Plica plica* and correctly concluded that the species should be placed in *Tropidurus.* To this I can only add that in every respect *bogerti* shows the characteristics of *Tropidurus* that I have used to distinguish that genus from *Plica.*

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Xref

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INTRODUCTION

THE Lycopteridae, a family of small (< 12 cm) upper Jurassic–lower Cretaceous teleosts, are widely distributed in lacustrine deposits of eastern Siberia, Mongolia and China (from 36°–56°N, and 96°–134°E).

Until Yakovlev's (1965) recent revision, the systematics of this family were in some disorder, with at least sixteen nominal species referred to the genus *Lycoptera*. In addition, a number of rather ill-defined genera were also recognized. Yakovlev's critical study suggests that there are only two species of *Lycoptera* (*L. middendorffi* Müller, 1848, and *L. fragilis* Hussakof, 1932), and that three other and monotypic genera should also be recognized (*Manchurichthys*, *Sinolycoptera* and *Mesoclupea*). Compared with *Lycoptera* these genera are poorly studied, and contribute little to understanding the phyletic relationships of the family. Thus, for the purposes of this paper references to the lycopterids are, in fact, to the genus *Lycoptera* itself.

Apart from Reis' (1910) observations on the otoliths of *Lycoptera middendorffi* (and some notes on vertebral structure by Saito [1936]), no really comprehensive anatomical study appeared until Berg's revision of the family was published in 1948. Thus it is not surprising that the systematic position of the Lycopteridae has been in some doubt ever since the family was defined by Cockerell (1925). Yakovlev's (*op. cit.*) remarks that " *Lycoptera* has to this day remained the most interesting and enigmatic fish of the Asian Mesozoic ", are fully justified, particularly when it is recalled that *Lycoptera* has been considered the ancestor or near ancestor of the Cyprinidae. If this relationship could be accepted, then the lycopterids might also throw some light on the origin of the largest and most diverse group of freshwater fishes, the Ostariophysi.

It was mainly from this viewpoint (see Rosen and Greenwood, 1970) that I began to study the Lycopteridae in detail. Soon it became clear, however, that the lycopterids and the cyprinids (or for that matter any member of the Ostariophysi) were in no way related, a conclusion reinforced by the appearance of Gaudant's (1968) paper dealing at length with the anatomy of *Lycoptera davidi* (= *L. middendorffi*).

Several features in the osteology of *Lycoptera* suggested a relationship with the osteoglossomorph family Hiodontidae. It is the object of this paper to review the osteology of *Lycoptera* (particularly since I disagree with Gaudant [*op. cit.*] on certain points), and in the light of that review to compare the two families and reconsider the various proposed relationships of the Lycopteridae.

The only fossil hiodontid, *Eohiodon rosei* (Hussakof), from the middle Eocene beds of British Columbia (see Cavender, 1966a) closely resembles *Hiodon* in most anatomical features. References to *Hiodon* thus include *Eohiodon* as well as the two extant species of *Hiodon*, *H. alosoides* and *H. tergisus*. Where *Eohiodon* resembles, or departs from *Lycoptera* more than does either *Hiodon* species, then it will be given particular mention.

A COMPARISON OF *LYCOPTERA MIDDENDORFFI* WITH *HIODON* AND *EOHIODON* SPECIES

Study material : Information on *Lycoptera* osteology was derived principally from eight well-preserved specimens of *L. middendorffi* in the collections of the British Museum (Nat. Hist.) Palaeontology Department (specimen numbers P16967a and b, and P20930) ; forty-eight less well-preserved specimens from the same slabs also provided some information, as did three specimens kindly loaned to me by the Munich Museum.

Most of the *Hiodon* material examined is of *H. alosoides* (27 specimens) but some *H. tergisus* (11 specimens) were also studied ; dissections, dried skeletons, alizarin transparencies and radiographs were used. The size range of these fishes is 2·5 to 26·0 cm standard length. All are from the B.M. (N.H.) collections.

Neurocranium (Text figs. 1 to 4). The nature of the *Lycoptera* fossils is such that it is impossible to prepare a complete, three-dimensional neurocranium. Consequently, any comparison is restricted to superficial regions of the skull. It is particularly regrettable that no observations could be made on the otic regions of the skull in these fishes since the otic region provides a highly characteristic and specialized feature of the hiodontids (Ridewood, 1904 ; Greenwood 1963, and in preparation).

Nasals. These bones are not well-preserved in most specimens. The few that I have been able to examine are narrow, slightly curved, gutter-like elements closely associated with and separated by the median ethmoid.

In *Hiodon*, the nasals are tubular, and more strongly curved (indeed, are angled). As in *Lycoptera* they are associated with the median ethmoid, and posteriorly are in contact with the frontals.

Gaudant (*op. cit.*) likens the nasals of *Lycoptera* to those of *Elops saurus*, but in my opinion they are more like those of the Mormyridae. In *Elops* (and other elopoids, see Nybelin 1956 and 1967) the sensory canal is contained within a tube provided with four pores, and the base of the nasal is expanded to a greater (*Elops* and *Megalops*) or lesser (*Tarpon*) degree. In contrast, the mormyrid nasal is an open gutter (personal observations ; Taverne 1968 and 1969 ; Ridewood, 1904).

Yakovlev (1965) on the other hand, describes the nasals of *Lycoptera* as " . . . contiguous and not divided by the frontal bones . . . , even in the posterior third . . . " I would agree that the frontals probably do not separate the nasals, but in no specimens can I find evidence of the nasals being contiguous at any point. Judging from the shape of the anterior frontal tips it is even possible that a short region of each frontal lies between the posterior part of the nasals (personal observation ; and see Gaudant's plate 4, figs. 1 and 2). The supposed contiguity of the nasals is one of the reasons why Yakovlev (*op. cit.*) thought that *Lycoptera* might be related to the osteoglossids (see page 282).

Median ethmoid : Lying between the nasals is a relatively small, almost rectangular bone identified as a rostral by Berg (1948), and as a rostro-postrostral by Gaudant (*op. cit.*). Yakovlev (*op. cit.*) refers to a rostral in *Lycoptera* (but gives no description of the bone), and uses its presence as part of an argument to show that the ethmoid region in *Lycoptera* is more primitive than in *Leptolepis coryphaenoides*.

From my own observations (on admittedly few and, for that region, poorly preserved specimens) and from Gaudant's figures and plates, I can see no reasons for identifying the bone as a rostral (see Gardiner, 1963 and Nybelin 1967 for discussion). There is no trace of a transverse rostral commissure (*pace* Berg, *op. cit.*), nor does the arrangement of the circumorbital bones suggest that one was present. Gaudant (*op. cit.*) tentatively identifies, in one of his specimens, an ethmoidal pit line, but in none does he mention a tubular commissure ; none is visible in any of his figures.

Thus, I would propose that this bone be identified as a median ethmoid. Its shape and spatial relationships are like those of the median ethmoid in *Hiodon*.

Orbital region (Text figs. 1 and 2). Little can be learned about the orbital region in *Lycoptera*. The orbitosphenoid is somewhat smaller than in *Hiodon* ; the pterosphenoid and basisphenoid have not been clearly defined although faint indications of both are sometimes visible.

A long, splint-like supraorbital bone has been identified by Berg (1948) and by Liu *et al* (1963). Gaudant (*op. cit.*), however, failed to find this element, and I would agree with his conclusion that it is wanting in *Lycoptera. Hiodon,* too, lacks a supraorbital (as do all the Osteoglossomorpha).

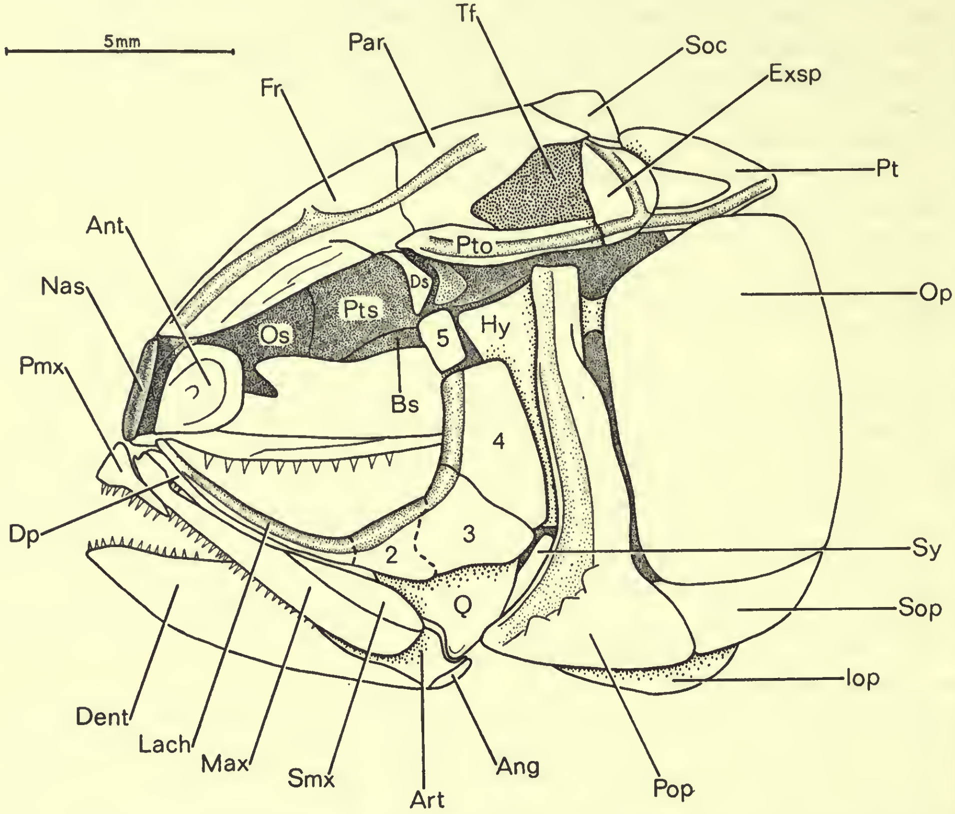

Fig. 1. *Lycoptera middendorffi.* Skull slightly restored; based mainly on specimen B.M. (N.H.) P20930 I. Lateral line canals of extrascapular from Berg (1948) and Gaudant (1968); canals in dentary omitted. The endopterygoid is not shown. The margins of the 2nd infra-orbital bone are indicated by dotted lines.

Ang. angular; Ant. antorbital-prefrontal; Art. articular; Bs. basisphenoid; Dent. dentary; Dp.? dermopalatine; Ds. dermosphenotic; Epi. epiotic; Exsp. extrascapular; Fr. frontal; Hy. hyomandibula; Ic. intercalar; Iop. interoperculum; Lach. lachrymal; Max. maxilla; Meth. median ethmoid; Mth. metapterygoid; Nas. nasal; Op. operculum; Os. orbitosphenoid; Par. parietal; Pmx. premaxilla; Pop. preoperculum; Pt. posttemporal; Pto. dermopterotic; Pts. pterosphenoid; Q. quadrate; Smx. supramaxilla; Soc. supraoccipital; Sop. suboperculum; Sy. symplectic; Tf. temporal fenestra. 2–5. 2nd to 5th infraorbitals.

Frontals: (Text figs. 3 and 4). In their general outline and relative contribution to the dorsicranium, the frontals of *Lycoptera* and *Hiodon* are similar (see below, p. 271, regarding the sensory canal systems). Whether or not in *Lycoptera* the anterior tips of the frontals lie between the nasals, is uncertain (see above, p. 261).

Parietals (Text figs. 3 and 4). The entire outline of these bones is not clearly defined in any of the B.M. (N.H.) specimens. However, from the observations I could make, I would agree with the restorations figured by Gaudant (*op. cit.*). The shape of the parietals in *Lycoptera* and *Hiodon* is not markedly different. But, in *Hiodon* the supraoccipital is a much larger bone with a greater anterior extension ; consequently the area of medial contact between the parietals is much less than in *Lycoptera* (*cf.* text figs. 3 and 4).

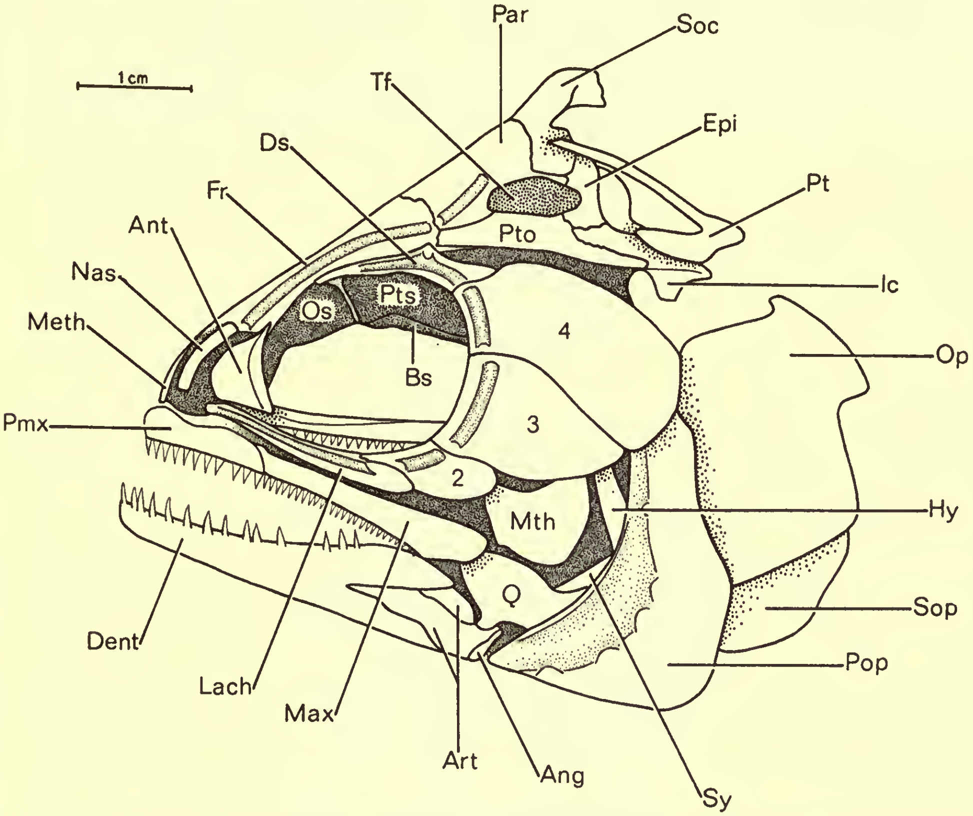

FIG. 2. *Hiodon alosoides*. Skull. Endopterygoid, and lateral line canals of dentary omitted. The extrascapular has been removed to show the parietal, and the temporal fenestra. Abbreviations as in fig. 1.

Temporal fenestra. A large temporal fenestra is visible in all B.M. (N.H.) specimens of *Lycoptera* in which that region of the skull is well-preserved. Gaudant (*op. cit.*) also found this opening in his material. Liu *et al* (1963), however, illustrate the dorsicranium of a specimen (size not stated) in which no fenestra is present. Gaudant suggests that Liu's fish may be a very large individual, and that with growth the bones surrounding the fenestrae encroach upon, and eventually obliterate the openings completely. No specimens with fenestrae in an intermediate stage of closure have been illustrated or noted, and there remains the possibility that Liu *et al* overlooked the fenestrae in their material. Even in the best specimens the fenestral outline is faint.

Gaudant (*op. cit.*) describes the temporal fenestra as being bordered by the parietals, dermopterotic, extrascapular and supraoccipital. Some of these bones are undoubtedly associated with the fenestra, but since the extrascapular lies above the opening (text figs. 1 and 3) it can hardly be considered one of the delimiting bones. Also, from my own observations I am uncertain whether the supraoccipital is involved. A small area of the medial margin, which Gaudant identifies as part of the supraoccipital, appears to be a narrow, posterior prolongation of the parietal (see text fig. 3). Finally, I would identify the posterior boundary of the fenestra as being the epiotic ; from Gaudant's figure and description he implies that the extrascapular forms that border. In at least two B.M. (N.H.) specimens the extrascapular is displaced and the epiotic can be seen forming the hinder limit of the fenestra.

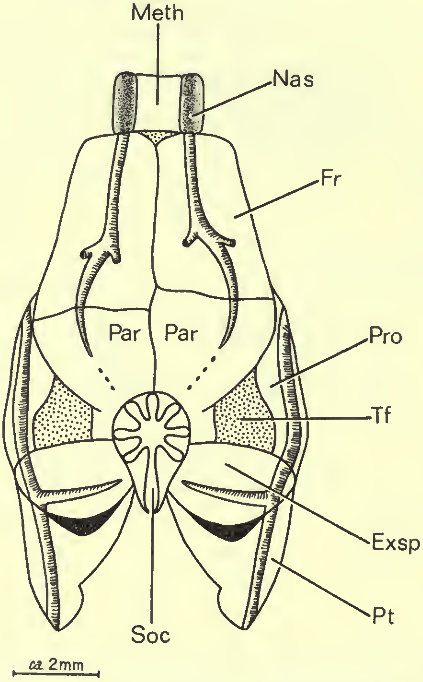

FIG. 3. *Lycoptera middendorffi.* Dorsicranium. Modified after Gaudant (1968). Abbreviations as in fig. 1, except Pro. pterotic.

The significance and homology of the temporal fenestra are difficult to establish. As Ridewood (1904) noted, it would appear to correspond with the preepiotic fossa found in most clupeoid fishes. This fossa is a small but deep pit lying immediately anterior to the epiotic, and is formed by an invagination from the parietal, epiotic and autopterotic. There are, however, differences in the two structures. The clupeoid preepiotic fossa usually ends blindly against the deeper part of the supraoccipital and is a distinct pit in the bones involved. The temporal fenestra does not involve invagination of the bones, and if it were not closed by cartilage, would open directly into the cranial cavity.

A temporal fenestra similar to that of *Lycoptera,* (albeit less extensive) occurs in *Hiodon,* where it is occluded by a plug of cartilage. In *H. alosoides* the fenestra is largest in small fishes, but is still clearly visible in the largest specimen examined (26 cm S.L.). It is filled by a slip of epaxial body musculature and the whole area is covered by the greatly expanded extrascapular (*cf. Lycoptera* where the extrascapular only covers the posterior quarter of the fenestra.)

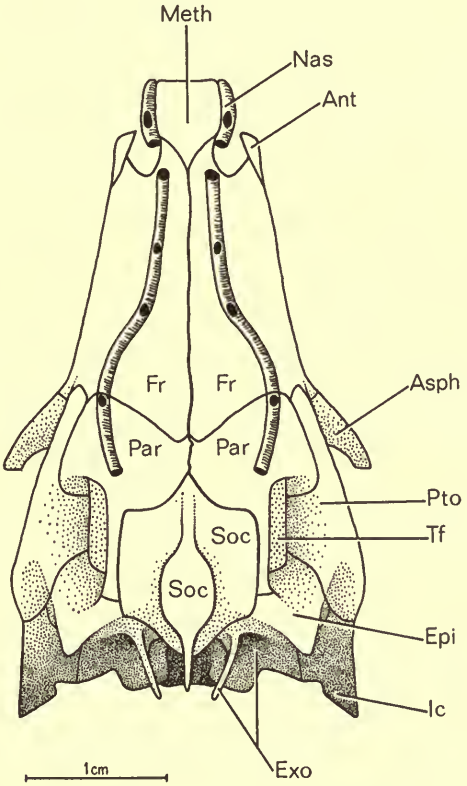

FIG. 4. *Hiodon alosoides.* Dorsicranium. The plane of orientation is such that a line drawn through the centre of the basioccipital facet to the vomer, would be horizontal. Asph. autosphenotic ; Exo. exoccipital. Others as in fig. 1.

As Gaudant (*op. cit.*) points out, the temporal fenestra is an unusual character, and one not found in any other Mesozoic teleost. Indeed, *Lycoptera* and *Hiodon* would appear to be the only primitive teleosts in which a temporal fenestra is developed (see also Greenwood, 1963). The large cartilaginous area in the temporal region of salmonoid and galaxioid fishes (the 'temporal fossa' of McDowall, 1969) resembles the temporal fenestra but is a more extensive, less well-defined area bordered by more (and often intrasubordinally different) bones ; it would seem to be a correlate of the generally reduced ossification of the salmoniform skull.

Undoubtedly the development of a temporal fenestra (*Lycoptera* and *Hiodon*) or preepiotic fossa (Clupeoidei) is associated with the invasion of that part of the skull by epaxial body muscles. That a fossa is developed in clupeoids and a fenestra in *Hiodon* and *Lycoptera* may indicate that the structures are more probably analogous than homologous. Certainly there is no evidence from other characters to suggest a close relationship between the clupeoids and hiodontids (Greenwood, 1963 ; Greenwood *et al*, 1966).

In *Lycoptera* only the posterior part of the temporal fenestra is covered by the extrascapular, whilst in *Hiodon* the entire fenestra (and most of the parietal) lies beneath the expanded, scale-like extrascapular. Thus both the relative size, and the shape of this bone differ in the two genera. Another difference is the arrangement of the extrascapular latero-sensory canals. *Lycoptera*, according to Berg (1948) and Gaudant (*op. cit.*), had the posterior section of the temporal canal (*i.e.* the section between the posttemporal and the pterotic) passing through the lower part of the extrascapular (see text fig. 1). The branch forming the transverse commissure is given off near the hind margin of the bone, and runs medially in that position. (None of the B.M. (N.H.) specimens has this region of the skull sufficiently well-preserved to allow for first-hand observation on these points). In *Hiodon*, the branch from the posttemporal connects with the dermopterotic directly, and the extrascapular carries, near its posterior margin, the transverse commissure only. Both genera are alike in having the bony tube for the transverse commissure interrupted in the midline because the extrascapulars are separated by the supraoccipital. The gap is wider in *Lycoptera* than in *Hiodon*.

The otico-temporal region. The *pterotic* is an elongate and substantial bone in both genera. As far as I can determine, the temporal latero-sensory canal in *Lycoptera* is entirely bone enclosed ; in *Hiodon* the ventromedial aspect of the tube is open (Greenwood, 1963).

Virtually nothing is known about the occipital and lower otic regions of the *Lycoptera* skull, since that region is invariably covered by the collapsed operculum and associated bones.

From Gaudant's description and figures (especially plate 3) it is clear that the *supraoccipital* in *Lycoptera* is a smaller bone than in *Hiodon*, and that it does not separate the parietals for such a distance anteriorly. The supraoccipital crest in *Lycoptera* appears to be lower and probably does not have the characteristically " T " shaped section of *Hiodon*. However, judging from Gaudant's plate the crest may have a short-armed " T " section.

The presence of a moderately large supraoccipital in the *Lycoptera middendorffi* specimens figured by Gaudant (*op. cit.*) makes it the more difficult to understand the minute bone (not separating any part of the parietals, and hardly separating the extrascapulars) illustrated by Liu *et al* (1963, fig. 8). It will be recalled (p. 263) that these authors do not show a temporal fenestra in this fish, which Gaudant suggested might be a large individual in which the fenestrae had closed. Unfortunately Liu *et al* give no indication of the size of the specimen (nor any magnification for the figure), neither do they discuss the supraoccipital in the text of their paper ; no dorsicranium is figured in the plates. That a fenestra might be obliterated by growth is a reasonable assumption, but it is improbable that parietal growth would almost cover the supraoccipital. I am inclined to think that Liu *et al*, probably influenced by the relationships of these bones in *Leptolepis*, have misinterpreted the situation in *Lycoptera* (*cf.* their drawings of these skulls in figure 8).

Skull base (Text figs. 5A and B). The *parasphenoid* is toothed in both genera with the teeth relatively larger and extending further posteriorly in *Hiodon* (and probably in *Eohiodon*). A small basipterygoid process is present in *Lycoptera*, but is absent in *Hiodon*. Gaudant (*op. cit.* plate 5, figs. 3 and 4) illustrates the posterior half of the parasphenoid in *Lycoptera middendorffi*, and clearly demonstrates its sharp upward angling (*ca.* 45°), a little posterior to the foramen for the internal carotid (see text fig. 5B). His photographs also show the relatively short, paired and near vertical ascending processes of this bone. These come into contact with the prootic, while the section running obliquely upwards forms the ventral, unpaired part of the base underlying the otico-occipital region of the skull.

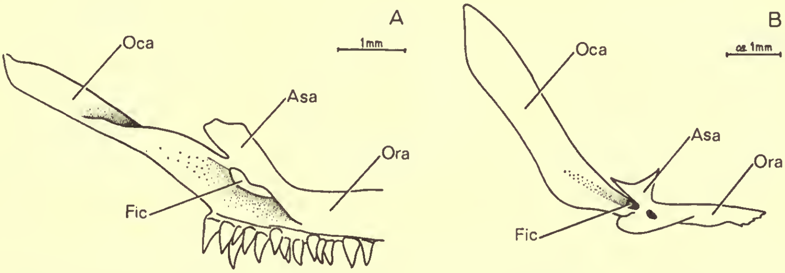

FIG. 5. *A. Hiodon alosoides.* Posterior part of a parasphenoid, viewed from the right. *B. Lycoptera middendorffi.* Posterior part of parasphenoid, viewed from the right (after Gaudant, 1968 : plate 5, fig. 4). Asa. ascending arm ; Fic. foramen for internal carotid artery ; Oca. occipital arm ; Ora. orbital arm.

The shape of the parasphenoid and the details of its morphology (except for the basipterygoid processes) are very similar in *Lycoptera* and *Hiodon* (see text fig. 5). Thus it seems reasonable to conclude that the ventral skull profile in *Lycoptera* had the same, peculiar " stepped " appearance as in *Hiodon*.

Otoliths (Text figs. 6 A-C). The peculiar otoliths of *Lycoptera middendorffi* were described and illustrated with great thoroughness by Reis (1910). In most of his specimens two of the three otoliths from each side (and sometimes from both sides) were preserved, if not *in situ*, at least closely associated with the skull. Accordingly Reis was able to determine the approximate spatial relationships of the otoliths, and on this basis to show that the asteriscus (lagenar otolith) is much larger than the sagitta (saccular otolith). From Reis' drawings and descriptions, the asteriscus is about 4 to 6 times longer than the sagitta. It also has an unusual, trapezoidal or unequally hexagonal outline. The shape of the sagitta is difficult to determine from the figures, but it appears to be trianguloid and without any marked sculpturing. The asteriscus, by contrast (text fig. 6C) has each face radially fluted over about half its area, and there is at least one, short, crescentic groove at a point about two-thirds distant from the lower border (as orientated in the figures). Ornamentation seems to be more obvious on one face than on the other. No otolith was identified (or shown in a drawing) as a lapillus (utricular otolith) and Reis (*op. cit.*) makes no comments on its absence.

As Reis points out, it is most unusual among teleosts for the asteriscus to be larger than the sagitta, a condition otherwise found only in the Ostariophysi (and to a somewhat less marked degree in the Mormyridae, see Taverne, *op. cit.*) In both these groups, the shape of the sagitta and asteriscus is quite unlike their presumed counterparts in *Lycoptera*. Indeed, a large, hexagonal-trapezoidal asteriscus has, to the best of my knowledge, never been described from any other teleost group. Furthermore, the peculiar radial fluting of the *Lycoptera* asteriscus has not been described elsewhere.

Later workers (Saito, 1936 ; Takai, 1944 ; Berg, 1948 ; Liu *et al* 1963) do not describe otoliths from their material. When the otoliths are mentioned by these authors, it is always with reference to Reis' (1910) paper and figures. Gaudant (*op. cit.*) found otoliths in only one of the specimens he examined (L. *middendorffi*, B.M. (N.H.) reg. no. P273 [now P47792] ; but see below). His comments on *Lycoptera* otoliths, like those of his predecessors, are also based on Reis. (It should be noted that Gaudant reproduces one of Reis's drawing of an asteriscus but in the legend to the figure calls it a sagitta).

None of the B.M. (N.H.) specimens has the otoliths preserved, and I was unable to find them in specimen P47792 (where, according to Gaudant [*op. cit.*], they should be visible). I have tried to locate Reis' material, but without success. Apparently it is now either lost or destroyed. The absence of suitable material for otolith studies is the more regrettable because certain features of the otoliths described by Reis (*op. cit.*) suggest that his identification of the larger element as an asteriscus may be in error.

Compared with the sagitta, far less is known about intergroup variation in the shape of the teleost lapillus and asteriscus. Nevertheless, some generalizations on this subject are possible (based on Retzius, 1881 ; Frost, 1925–1930 ; Taverne, 1968 and 1969 ; and personal observations).

Apart from in the Ostariophysi and the Mormyriformes, the asteriscus is generally a flattened, slightly elongate, often kidney-shaped otolith with all or most of its margin deeply crenulate (often almost serrate) ; there is a deep and extensive sulcus on the median face. In the Ostariophysi and Mormyriformes the asteriscus is usually discoidal, the broad sulcus horseshoe-shaped, and the margin variously crenulate, serrate or smooth (or a combination of all three). A few ostariophysans have an elongate asteriscus which closely resembles the " typical " sagitta of other groups.

The angular, trapezoidal to hexagonal outline of the so-called asteriscus in *Lycoptera* has not yet been found in any teleost. Neither does the *Lycoptera* " asteriscus " have the prominent sulcus characteristic of that otolith in most (if not all) teleosts. Reis (*op. cit.*) attempts to identify a sulcus, but it is clear from both his description and figures that the feature he is dealing with is more in the nature of an elongate pit than the typically deep, extensive groove of the asteriscal sulcus.

A trapezoidal, or at least a noticeably angular outline appears to be more characteristic of the teleost lapillus (utricular otolith). Furthermore, that otolith does not show a well-developed sulcus, and its marginal ornamentation is often in the form of rather widely spaced radial grooves extending towards the centre of the otolith. On the upper face of the lapillus (near the region where the radial grooves converge) there is frequently a shallow, depressed area lying close to a low dome or ridge (text fig. 6A).

Altogether, the so-called asteriscus of *Lycoptera* shows more of the characters of a lapillus than an asteriscus. I am especially impressed by the resemblance between the *Lycoptera* " asteriscus " and the lapillus of *Hiodon alosoides* (*cf.* text figs. 6A and B with 6C, and with the figures in plate 2 of Reis, 1910). This resemblance includes the outline shape as well as many details of ornamentation, including the spaced radial grooves (more numerous over one half of the otolith) and the absence of a well-defined sulcus. Thus, I suspect that Reis misidentified the lapillus in *Lycoptera* as an asteriscus.

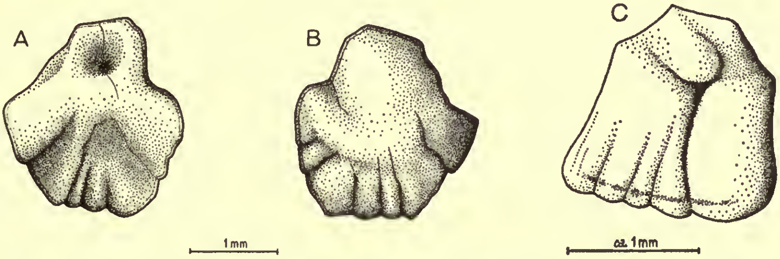

FIG. 6. A, B. *Hiodon alosoides*, lapillus in dorsal and ventral views. C. *Lycoptera middendorffi*, " asteriscus " (after Reis, 1910, plate 2, fig. 11)

There remains, however, the problem posed by the disposition of the otoliths as Reis has figured them in relation to the skull (Reis, *op. cit.*, plate 2). The problem is complicated by the lack of a third otolith in any specimen figured. In *Hiodon* the lapillus lies above and well anterior to the sagitta and asteriscus. One would, therefore, expect that in a fossil (even allowing for some *post mortem* dislocation) the lapillus should lie ahead and slightly above the other two otoliths (or the sagitta alone if that is the only lower otolith visible). In Reis' figures, the larger " asteriscus " is always shown behind the smaller otolith (his sagitta), and generally above it. The labyrinth of *Hiodon* is unusual in having the lapillus so far in advance of the sagitta ; in most fishes the lapillus lies above or even slightly behind the sagitta. If this latter condition was found in *Lycoptera*, then it would be possible for the sagitta to come to lie in front of the lapillus. Also, if *Lycoptera* had a large auditory fenestra (as in *Hiodon*) lateral to the sacculus, it seems even more likely that the sagitta could be displaced anteriorly during fossilization. The bone enclosed lapillus would be less subject to horizontal displacement.

I have of course assumed, as did Reis, that the smaller otolith is a sagitta. This point also remains to be clarified ; the figures and descriptions given by Reis (*op. cit.*) are not sufficiently clear for a decision to be made. The sagitta of *Hiodon alosoides* is a most peculiar otolith and it should be possible to recognize its salient features in well-preserved fossils. All that can be said at present is that no features visible in Reis' drawings would immediately preclude the smaller otolith from being of the *Hiodon* sagitta type.

The so-called lycopteroid otoliths from the Mesozoic of Germany (Weiler, 1954, 1957 and 1965) are not closely similar to those of *Lycoptera middendorffi* (see page 283).

Circumorbital bones (Text fig. 1). Because the circumorbital series is generally not well preserved, little agreement has been reached on the number or the shape of these bones (*cf.* Berg, 1948, fig. 1 ; Liu *et al*, 1963, fig. 8 ; Gaudant, 1968, fig. 3.).

Berg (*op. cit.*) illustrates a single, elongate suborbital bone lying between the canal-bearing infraorbital series and the preoperculum. From Gaudant's (*op. cit.*) study, and from my own observations it is certain that Berg was in error. No suborbital is present ; the circumorbital series in *Lycoptera* is typically teleostean and is composed solely of canal-bearing infraorbital bones.

Judging from the two B.M. (N.H.) specimens (both on slab P20930) and from Gaudant's plate 2, fig. 1, Liu *et al*'s (*op. cit.*) restoration is the most accurate so far published. Certainly Gaudant's text fig. 3 is inaccurate in some respects. For example, the postorbitally situated infraorbitals are considerably wider than he depicts them, and the lachrymal (1st infraorbital) is much longer (see text fig. 1).

From my material I cannot be certain whether there are one or two bones lying below the orbit (Berg figures two and part of a third, Liu *et al* three, and Gaudant three and part of a fourth). Be that as it may, the first infraorbital (lachrymal) is a narrow, elongate bone deepening a little (or more definitely if there is no small second infraorbital) posteriorly. Behind the orbit there are two deep and wide bones, which extend backwards almost to the margin of the preoperculum. Above these it is difficult to determine the number or shape of the succeeding infraorbitals. In specimen P20930 there appears to be a short, barrel-shaped bone followed by an elongate, almost boomerang-shaped dermosphenotic.

Anteriorly, a large, shield-shaped antorbital is apparently fused with the prefrontal. Berg (1948) and Liu *et al* (1963) identify this bone as the lateral ethmoid, but it is clearly a canal bearing bone with another ossification lying medial to it (which I identify as being the prefrontal). My reason for thinking that the antorbital and prefrontal are fused is simply that the two bones (in all specimens I have examined) always have the same relative positions ; the other infraorbital bones are invariably displaced and variously disarticulated.

The bone Berg (*op. cit.*) identifies as a dermosphenotic (*i.e.* the uppermost infraorbital) is roughly triangular, as is the dermosphenotic in Gaudant's (*op. cit.*) restoration. A bone occupying a similar position in my best preserved specimen (P. 20930) is much narrower and is boomerang-shaped, the concave face directed anteriorly (text fig. 1). But, as there is only one specimen with a presumed dermosphenotic visible, I could well be mistaken on this point.

Regarding the total number of infraorbital bones (including the dermosphenotic and antorbital), Berg (*op. cit.*) finds 7 (*i.e.* interpreting his lateral ethmoid as an antorbital), Liu *et al* 6 (again interpreting the lateral ethmoid as an antorbital), and Gaudant (*op. cit.*) 6. However, Liu *et al* do not specifically identify a dermosphenotic (which they do in the *Leptolepis* they figure) ; from their drawing it seems likely that a 7th infraorbital (*i.e.* a dermosphenotic) is present. The count from specimen B.M. (N.H.) P20930 could be either 6 or 7 depending on whether or not the small " second " infraorbital is a preservation artefact.

Hiodon has a total of 6 infraorbital bones (Nelson, 1969). Although there is an overall similarity between *Hiodon* and *Lycoptera* in the shape of the entire series (narrow suborbitally, expanded postorbitally) there are differences in detail (*cf.* text figs. 1 and 2). The expanded postorbital bones are deeper in *Hiodon*, and the infraorbital preceding the dermosphenotic is expanded (short and narrow in *Lycoptera*). The antorbital in *Hiodon*, like that of *Lycoptera*, is fused with the prefrontal, and the dermosphenotic is an elongate, angled bone (larger than, but basically similar to *Lycoptera*).

Cephalic lateral line system (Text figs. 1 to 4). Superficially, the cephalic lateral line system is virtually identical in both *Lycoptera* and *Hiodon*. It is of the primitive type in which there is no connection between the supraorbital and temporal canals ; the infraorbital canal is connected, through the dermosphenotic, with the temporal canal in the dermopterotic, but the supraorbital system ends in the parietal. The supraorbital canal has medial and lateral branches in *Lycoptera*, but these are not developed in *Hiodon*.

Other differences concern branching of the infraorbital system. In *Hiodon* this canal divides in the dermosphenotic, one branch curving backwards to join the temporal canal, the other and longer branch running forward in the dermosphenotic below and parallel with the supraorbital canal in the frontal. No such dichotomy has been described in *Lycoptera*.

In *Hiodon*, the pterotic portion of the temporal canal is open medially for much of its length (Greenwood, 1963) and forms part of what appears to be a pseudo *recessus lateralis* (in connection with which other bones, including the hyomandibula, are modified ; personal observations). Unfortunately the nature of the pterotic canal cannot be determined in *Lycoptera* (or in *Eohiodon*).

Opercular series (Text figs. 1 and 2). The *preoperculum* of *Lycoptera*, compared with that of *Hiodon*, and especially *Eohiodon*, has a more pronounced posterior prolongation of its lower, horizontal arm which is also shallower than in *Hiodon*. The vertical arm is longer, and reaches the pterotic ; in *Hiodon* there is a distinct gap between the two bones. Expressed in another way, the preoperculum in *Lycoptera* extends vertically beyond the hyomandibula head, whereas in *Hiodon* it barely reaches the level of the opercular process on the hyomandibula.

The *operculum* of *Lycoptera* is a relatively larger bone and extends further dorsally than it does in *Hiodon* ; in that genus its upper margin is excavated, not rounded as in *Lycoptera*.

The *interoperculum* of *Lycoptera* appears to be more ventrally situated because it is visible in lateral view, whereas in *Hiodon* it is hidden behind the ventral limb of the preoperculum. There are also differences in the shape of the *interoperculum*. In *Hiodon* the bone is almost rectangular, is narrow and nearly as long as the horizontal arm of the preoperculum. In *Lycoptera* it is relatively shorter (about half the length of the preoperculum), is somewhat deeper, and has a curved lower margin.

The *suboperculum* is similar in both genera.

Hyoid arch (Text figs. 7A and B). The hyoid arch of *Lycoptera middendorffi* has been described in great detail by Gaudant (*op. cit.*). The *hyomandibula* differs from that of *Hiodon* in several respects. Both, however, have a very well-developed opercular process, but this is probably of little significance since a large process is found in such unrelated groups as the esocoids and gadoids, as well as in the osteoglossoids and notopteroids. *Lycoptera* has a single articular head to the hyomandibula ; in *Hiodon* this surface is double with a large but bridged gap between each head (an arrangement probably correlated with the pseudo *recessus lateralis* mentioned above).

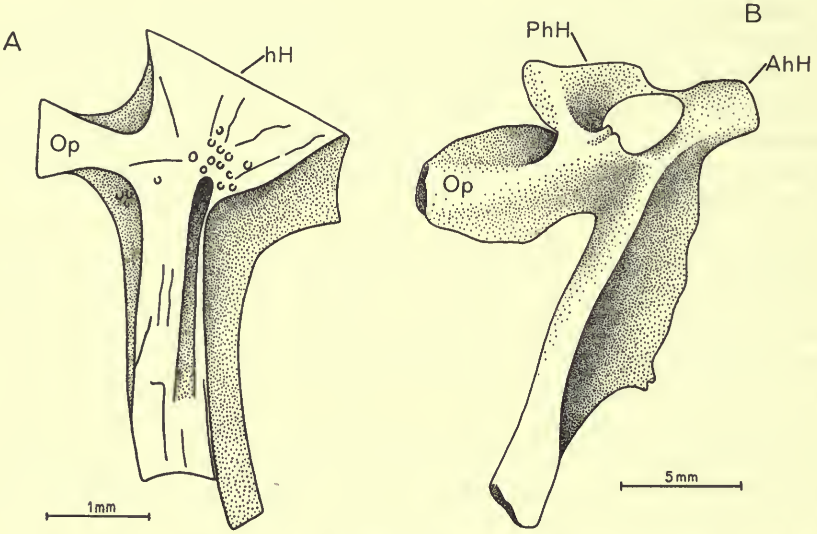

FIG. 7. A. *Lycoptera middendorffi.* Right hyomandibula, lateral aspect (after Gaudant, 1968). hH. head of hyomandibula ; Op. opercular process. B. *Hiodon alosoides.* Right hyomandibula, lateral view. AhH. anterior head ; PhH. posterior head ; Op. opercular process.

The shape of the *ceratohyal,* as well as the shape, number and disposition of the branchiostegal rays (especially the three, curved, broad upper rays) are closely similar in both *Lycoptera* and *Hiodon.* It may be noted in passing that in these characters neither genus resembles either the elopoid or clupeoid types ; perhaps the closest resemblance is to the notopterid and mormyrid types (McAllister, 1968).

Gaudant (*op. cit.*) describes and figures a single *hypohyal* in his specimens, but Berg (1948) found two small hypophyals. Unfortunately, this area of the hyoid arch is not clearly visible in any B.M. (N.H.) specimens. *Hiodon* has a pair of hypophyals on each side.

Both genera have a well-developed *basihyal dentition,* but the shape of the basihyal and its tooth plate are not known in *Lycoptera.* This is regrettable, since Nelson (1968) has drawn attention to the peculiar (and apparently characteristic) shape of the tooth plate in *Hiodon* ; a similarly shaped plate is otherwise only known from the related Notopteridae (Nelson, *op. cit.*).

Palatopterygoid arch (Text figs. 1 and 2). Again, it is from Gaudant's (*op. cit.*) work that the most detailed descriptions are available (see his text fig. 8).

The *metapterygoid* of *Hiodon* is relatively smaller than that in *Lycoptera*, and is kidney-shaped, without the antero-dorsally directed flange which overlaps the endopterygoid in *Lycoptera*.

Gaudant (*op. cit.*) identifies a small, toothless bone lying above the ectopterygoid (and immediately anterior to the endopterygoid) as a *dermopalatine*. If he is correct (which I doubt), then *Lycoptera* differs from *Hiodon* where the dermopalatine is toothed, and lies anterior to—and is in a linear series with—the ectopterygoid. One B.M.(N.H.) specimen, P20930, shows medially and a little above the dorsal margin of the maxillary head, a short length of toothed bone (see text. fig. 1). It seems reasonable to identify this bone as the dermopalatine ; if this is correct, then it is similar to the dermopalatine of *Hiodon*.

The *ectopterygoid* is toothed in *Hiodon*, toothless in *Lycoptera* ; the *endopterygoid* is toothed in both genera.

The *quadrate* has a similar shape and proportions in both *Hiodon* and *Lycoptera*.

Jaws (Text figs. 1 and 2) There is an overall similarity in the upper and lower jaw elements of both genera.

The *premaxilla* is a small bone without traces of an ascending process ; it is relatively longer in *Hiodon*, and its articulation with the maxilla is a more intimate junction in that genus.

The *dentary* in *Hiodon* is more slender, and the coronoid region is shallower than in *Lycoptera*. I do not agree with Gaudant's (*op. cit.*, fig. 9) figure of the *articular*. In B.M. (N.H.) specimens the joint surface of the articular is a deep and clearly defined notch (not, as he shows it, an elongate concavity) closely fitting around the quadrate head.

The *angular* is a small bone in both genera. According to Ridewood (1904) there is no angular in *Hiodon*, but it is present in all the alizarin preparations I have examined.

A single *supramaxilla* is present in *Lycoptera*, but absent in *Hiodon*.

Gular plate. A large gular plate is present in apparently both species of *Lycoptera*. No trace of this bone was found in any of the many *Hiodon* specimens examined.

Vertebral column. Saito (1936) has given a detailed description of the vertebrae in *L. davidi* (= *L. middendorffi*) to which little can be added. Saito was also the first to detect ontogenetic changes in the centra, which are diplospondylous in small individuals but mostly monospondylous in larger fishes (> 50 mm S.L.).

According to Saito (*op. cit.*) and Gaudant (*op. cit.*), the neural and haemal arches of caudal vertebrae are fused with the centrum (neither author mentions the condition in abdominal vertebrae). In my material of *L. middendorffi* (size range 40–55 mm S.L.) I find that the first four preural vertebrae have autogenous haemal arches, but that haemal arches on the more anterior vertebrae are fused with the centra in fishes > 45 mm S.L. ; in smaller fishes all the haemal arches appear to be autogenous.

Gaudant (*op. cit.*) describes both epineural and epicentral intermuscular bones (the latter he calls epipleurals although they are in no way associated with the pleural ribs). Other authors (except Takai [1944] who failed to locate intermuscular bones in some specimens) mention only one pair of intermuscular bones per vertebra, but differ in their opinions as to whether the bones are epineural or epicentral in position ; all agree that intermuscular bones are not present posteriorly beyond the first four or five caudal vertebrae. Takai's confused nomenclature for structures associated with the vertebrae has been clarified by Yakovlev (1965), who shows that, in fact, one pair of intermuscular bones is present in all the *Lycoptera* " species " studied by Takai (*op. cit.*)

From the B.M. (N.H.) material studied, I would identify the intermuscular bones as epineurals. This material also suggests how Gaudant (*op. cit.*) came to describe both epineurals and epicentrals. The epineurals in *Lycoptera* are very elongate bones, and thus extend backwards across several vertebrae. If the distal end of the epineural is displaced ventrally (or the tip is broken off and slips downwards) it can look much like a short intermuscular bone arising from a centrum behind that from which it actually stems. Careful examination, however, usually enables one to trace the " epicentral " back to its origin as an epineural on an anterior vertebra.

The pleural (ventral) ribs articulate with the tips of the broad-based, triangular parapophyses fused with the centra.

In *Hiodon*, the vertebral centra are somewhat stouter structures than those of *Lycoptera*, but are essentially of the same primitive type with a relatively large notochordal foramen. No trace of diplospondyly can be detected, even in the smallest specimen examined (*H. alosoides* 25 mm S.L.) ; it would be of great interest to know something about the ontogeny of the vertebrae in *Hiodon*.

More neural arches are autogenous in *Hiodon* than in *Lycoptera* (the condition is unknown in *Eohidon*), since the arches of all abdominal vertebrae are free from their centra, as are the first two caudal neural arches. All haemal arches except those of the first and second preural centra and the first ural centrum, are fused to the centrum. As in *Lycoptera*, the left and right halves of each abdominal neural spine are usually separate, even in large fishes (*i.e.* 25 cm S.L.) ; in caudal vertebrae, however, the spine is always a single structure (separate halves are common in the anterior caudal vertebrae of *Lycoptera*, and occasionally occur in the posterior vertebrae as well).

The parapophyses in *Hiodon* are fused with the centra but are elongate and dagger-shaped. In contrast with *Lycoptera*, the pleural ribs articulate directly with the centrum a little behind the shaft of the parapophysis (Greenwood, 1963).

Yakovlev (*op. cit.*) tabulated the various counts obtained for the number of vertebrae in *Lycoptera* " species " and warned of the difficulties in obtaining exact figures (diplospondyly, state of preservation, etc.). The counts for total number of vertebrae range from 43–50 (No indication is given of whether or not all the vertebrae associated with the caudal fin skeleton are included in these totals) ; 18–24 anterior vertebrae carry pleural ribs, the first rib being associated with the third centrum. *Hiodon* (*i.e.* both species) has 55–58 vertebrae (excluding the two ural centra), of which 27 or 28 bear ribs (Data from 9 specimens) ; the first rib is associated with the third vertebra. Even allowing for difficulties in obtaining accurate counts in

Lycoptera it is reasonable to conclude that *Hiodon* has more vertebrae and ribs. (Another lycopterid, the monotypic genus *Sinolycoptera langshanensis* resembles *Hiodon* in having 58 vertebrae [Yakovlev, *op. cit.*]). *Eohiodon*, with 49 vertebrae has a lower count than either *Hiodon* species, and thus more closely resembles *Lycoptera*, although it may have slightly more caudal vertebrae (*ca.* 25, *cf.* 20–23 in *Lycoptera*); no information is available on the number of pleural ribs in *Eohidon* (Cavender, 1966a).

Both *Lycoptera* and *Hiodon* have slender and elongate supraneurals lying between the neural spines of all vertebrae from in front of the first, until about the second vertebra behind the dorsal fin origin.

Caudal fin skeleton (Text figs. 8, 9 and 10) Besides a few comments by Berg (1948) on the number of hypurals and epurals, no author before Gaudant (*op. cit.*) paid much attention to the caudal fin skeleton in lycopterids. The figures in Reis (1910), Saito (1936), Takai (1944) and Liu *et al* (1963) are schematic and provide no critical information. Liu *et al* (*op. cit.*) describe the caudal fin in *L. muroii* (a synonym of *L. middendorffi*) as a " . . . somewhat advanced character " (relative to other " species " of *Lycoptera*) but do not list any specific reasons for their statement.

Gaudant (*op. cit.*, pp. 26–28, fig. 14) gives a detailed figure and description, as well as an excellent photograph of the specimen on which these were based (see plate 2, fig. 2). As figured by Gaudant, the caudal skeleton of *L. middendorffi* resembles the elopoid type (Nybelin, 1963) but with certain differences.

Salient features in Gaudant's restoration are : a separate second ural centrum, seven hypurals, three epurals, a fully-developed neural spine on the first pre-ural vertebra, a reduced spine on the first ural vertebra, and the uroneurals (called urodermals by Gaudant) arranged in two sets (a lower one of three elongate bones, and an upper set of two [one moderately long, and other short]). This uroneural arrangement is peculiar. It is neither of the elopoid type (three lower and a single upper bone lying at an angle to, and overlapping the former), nor of the leptolepid type (lower set of four and an upper of three short bones with at least the first overlapping the lower set) ; see Nybelin (1963) and Patterson (1967). The alignment and size of the upper uroneural (Ur 5) in Gaudant's figure does not accord with any known teleost caudal skeleton type (see Monod, 1968), nor does the arrangement of a small upper uroneural lying below an elongate one.

I have examined six well-preserved caudal fin skeletons of *L. middendorffi*, *ca.* 45–50 mm S.L., and find that I disagree with Gaudant on two major points. It might be added that I find the specimen illustrated in Gaudant's plate (*op. cit.*, plate 2, fig. 2) to be essentially like those I have examined.

In the B.M. (N.H.) fishes there is a single epural (not 3) closely associated proximally with the short neural spine on the first ural vertebra (see text fig. 9). The second point of disagreement concerns the number, shape and disposition of the uroneurals. In all B.M. (N.H.) specimens I find only a single series composed of three or four elongate bones, the first three being of approximately the same length, the fourth somewhat shorter.

I suspect that Gaudant has confused with epurals the proximal ends of caudal fin rays, the bifid neural spines of preural vertebrae, and possibly, fragments of uroneurals. The uroneural arrangement he describes is probably the result, in part, of the uroneurals being broken and displaced. His " urodermal 5 " in plate 2, fig. 2, and in text-fig. 14, certainly looks like the distal portion of the 2nd or 3rd uroneural.

In other respects Gaudant and I agree on the anatomy of the caudal fin skeleton. We both find that there is a total of 18 principal caudal fin rays (1 unbranched and 8 branched rays in each lobe). The articulated fin rays of the upper lobe are preceded by about 10-spine-like procurrent rays ; there are 8 procurrent rays in the lower lobe.

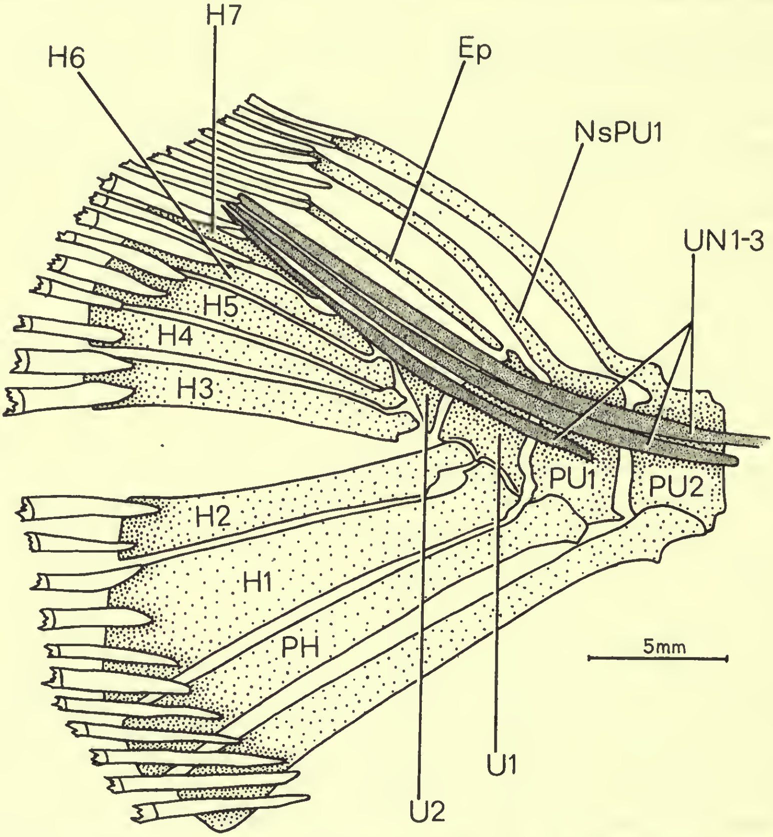

FIG. 8. *Hiodon tergisus.* Caudal fin skeleton, drawn from a radiograph of B.M. (N.H.) reg. no. 1862. 11. 18 : 45. For abbreviations see fig. 9.

Two of the six B.M. (N.H.) specimens have an interesting condition of the vertebrae associated with the 1st and 2nd hypurals (text fig. 10). Instead of there being a single first ural centrum carrying both hypurals, each hypural articulates with a separate centrum. The first caudal centrum carries a neural arch and short spine, the second an arch and very reduced spine. A third specimen (of about the same length as the other two, *ca.* 45 mm S.L.) has these two centra fused but with the fusion line still visible ; it resembles a caudal vertebra in the intermediate stage between diplo- and monospondyly. Those specimens with two distinct parts to the

" first " ural centrum also have a greater degree of displospondyly in the caudal vertebrae. Presumably the double " first " ural represents an early stage in the ontogeny of the usual compound first ural centrum. At first sight the double " first " ural centrum condition might be interpreted as comparable with the diplospondyly which occurs throughout the vertebral column in small fishes, and becomes progressively confined to the caudal region in larger individuals. However, there is an important difference between the two ural elements and a pair of hemicentra anteriorly. As Saito (*op. cit.*) demonstrated, in a diplospondylous caudal vertebra one hemicentrum of a pair (the anterior) is arch-less, while the other carries a neural and haemal arch and spine. The ural pair each has a neural arch and spine, as well as a hypural (modified haemal arch and spine). This suggests that each " first " ural element is a complete vertebra.

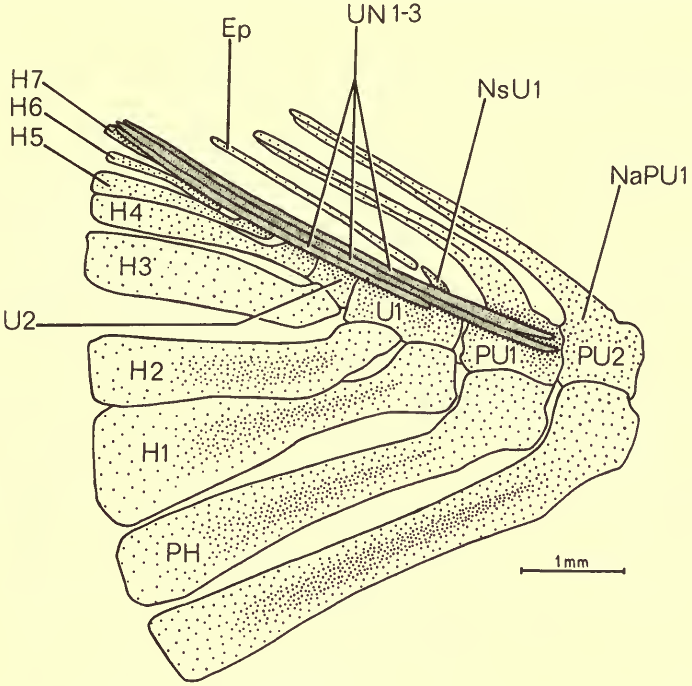

FIG. 9. *Lycoptera middendorffi*. Caudal fin skeleton, drawn from a latex cast of B.M. (N.H.) P16967b. Ep. epural ; H1–7 ; hypurals ; naPUI. neural arch of 2nd preural vertebra ; NsPU1. neural spine of 1st preural vertebra ; NsU1. neural spine of 1st ural vertebra ; PH. parhypural ; PU_1 ; PU_2, 1st and 2nd preural centra. U_1 ; U_2, 1st and 2nd ural centra. UN1–4, uroneurals.

There is no appreciable size difference between individuals with double and single first ural vertebrae. Perhaps, as Patterson (1967) suggested, *Lycoptera* shows individual variability in this character. Gaudant (*op. cit.*) believed that Patterson's observations could be attributed to poor preservation of the material. But I can certainly confirm that this is not so. Indeed, on one slab (P16967a) there are two specimens, overlapping one another, and both equally well-preserved ; in one fish there is a double " first " ural vertebra, in the other a single centrum.

When the first ural is a single element, only one neural arch and short spine is present, and the same condition is found on those apparently single centra with a clear-cut line of fusion still persisting. Also, when the centrum is a single element, its overall length is somewhat less than the two portions together. These observations seem to indicate that, if fusion is involved in the usual growth process, then there is a certain amount of resorption and remodelling of the bones.

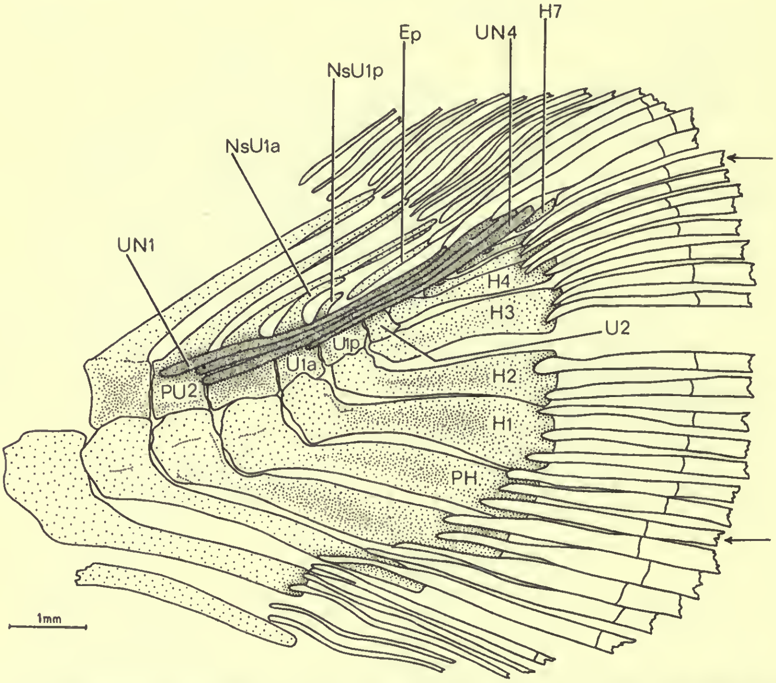

FIG. 10. *Lycoptera middendorffi.* Caudal fin skeleton (from P20930) to show the double " first ural " centrum. The first branched principal caudal ray of each lobe is indicated by an arrow. For abbreviations, see fig. 9 and NsU1a, NsU1p. neural spine on anterior and posterior elements of " first ural " centrum ; U1a and U1p. anterior and posterior components, respectively, of " first ural " centrum.

In all teleosts (as defined by Patterson, 1968) the first ural centrum always carries two hypurals and is therefore to be considered a compound element. The double condition found in certain *Lycoptera middendorffi* individuals would seem to be the retention of a primitive condition, a stage already lost in the other upper Jurassic and lower Cretaceous teleosts (*eg. Leptolepis, Thrissops, Allothrissops*). Other characters of the caudal fin skeleton in *Lycoptera, eg.* perichordally ossified centra, elongate uroneurals extending forward to the preural centra, two hypural support for the lower caudal lobe—preclude arguments that the skeleton is not teleostean.

Returning now to the overall morphology of the caudal skeleton in *Lycoptera.* If my interpretation of this structure is acceptable, there is a definite resemblance between the caudal skeleton in *Lycoptera* and *Hiodon* ; particularly in three important characters (*cf.* text fig. 8 with figs. 9 and 10).

First, there is agreement in the number of branched principal rays (16) ; other primitive teleosts (including *Leptolepis*) have 17 (*i.e.* 9+8). Sixteen rays are otherwise known from the Hiodontidae and most Mormyridae (see Nelson, 1969 for further discussion ; certain Galaxiidae with 16 rays [see McDowall, 1969] are irrelevant since the caudal skeleton in these fishes eliminates them from consideration as truly primitive teleosts).

Second, there is close similarity in the uroneural arrangement. In *Hiodon* and *Eohiodon* the 3 or 4 long uroneurals are arranged in a single series (that is, there is no upper series of one or more short uroneurals, as is typical for the lower teleosts). Certain other primitive fishes (*eg. Allothrissops, Thrissops*, ichthyodectids) also have only the lower set of uroneurals, but these are far more numerous (up to 7 ; see Patterson, 1967 ; Cavender, 1966b) than in *Hiodon* or *Lycoptera.*

Finally, in both *Lycoptera* and the hiodontids there is only one epural, a most unusual feature in lower teleosts. All other primitive groups (except perhaps the Osteoglossoidei, Notopteridae and Mormyridae, where the epural is probably absent, see discussion in Nelson, 1969) have three epurals (Patterson, 1968).

There is considerable variation is some aspects of the *Hiodon* caudal skeleton, especially in the number and development of neural superstructures associated with the first ural and preural vertebrae. For example, a fully developed spine on the first preural vertebra (present in *Lycoptera*) is not always developed, and the neural spine on the first ural is smaller than in *Lycoptera.* Nevertheless, the overall picture of variation for these characters in *Hiodon* and *Eohiodon* encompasses the condition found in *Lycoptera.* Most specimens of *H. alosoides* and *H. tergisus* have two neural arches on the first ural centrum, a condition reminiscent of that seen in some *Lycoptera,* but probably of no importance other than as a further indication of the compound nature of that vertebra.

Not only in general features, but in at least three critical characters the caudal fin and its supporting skeleton in *Lycoptera* is closer to that of *Hiodon* than to that of any other genus or group of fishes. Resemblances to the *Thrissops*—ichthyodectid caudal skeleton will be discussed elsewhere (but see Patterson, 1968, and Greenwood *et al,* 1966).

Fins and fin girdles. There is not enough information about the pectoral and pelvic girdles in *Lycoptera* for any meaningful comparisons to be made.

The *pectoral fin* of *Hiodon* spp., and *Eohiodon* is more expansive and falcate than that of *Lycoptera,* and has more rays (11–14, and *ca.* 13, *cf.* 9). *Lycoptera* has both the first and last rays enlarged, thickened and unbranched. In *Hiodon* only the first ray is unbranched and noticeably enlarged ; the lowermost ray has, however, a broad, fleshy extension of the membrane along its trailing edge. No details are available for this fin in *Eohiodon.*

Pelvic fin size, shape and area are similar in the three genera ; *Hiodon* species have 7 pelvic rays (the first unbranched), *Eohiodon* about 7 (no other details) and *Lycoptera* spp., 7 to 9.

The *median fins* in *Lycoptera*, *Hiodon* and *Eohiodon* are set well-back on the body ; fin outline is similar in the three genera, although the anal is longer in *Hiodon* (23–32 rays) than in *Lycoptera* (13–20, according to accounts in Yakovlev, 1965). Dorsal fin length is approximately equal (9–12 rays in *Hiodon*, 10–12 in *Lycoptera*). The dorsal fin ray count for *Eohiodon* (12 to 13) lies within the range for *Lycoptera*, as does the count for the anal (15 to 16 rays). In these characters *Eohiodon* shows a somewhat closer resemblance to *Lycoptera* than to *Hiodon*.

Scales. Cockerell (1925) used scale morphology in *Lycoptera* as a basis for defining the family Lycopteridae (as distinct from the Leptolepidae, in which *Lycoptera* had been classified previously). Although the scales of *Lycoptera* are distinctive *vis à vis* those of *Leptolepis*, Cockerell did note their close resemblance to the scales of the European Minnow *Phoxinus phoxinus* (thereby initiating the idea that lycopterids might be cyprinid ancestors).

Lycoptera scales are small, circular or slightly ovoid, with regularly arranged concentric circuli, with radii present basally and apically (the latter less well-defined than the former), and with a distinct, relatively large nucleus.

Hiodon scales are not similar. In outline they are almost thumbnail-shaped, with the anterior margin concave at each corner but convex medially (more so in scales from the flank than the dorsum) and with the laterobasal corners sharply rounded. The circuli are not arranged in circles since they bend to follow the outline of the margin. The nucleus is relatively small. Primary radii are confined to the anterior field, and are more numerous than in *Lycoptera* scales.

Little is known about the scales of *Eohiodon* (see Cavender, 1966a, page 317.)

DISCUSSION

SUMMARY OF ANATOMICAL FEATURES. Many characters shared by *Lycoptera* and *Hiodon* are characteristics of primitive teleosts, and thus are of little value in establishing relationships. Among these are :

1. The arrangement and relationship of bones in the dorsicranium (but see below regarding the temporal fenestra).
2. The pattern of the cephalic lateral line system.
3. Presence of teeth on the parasphenoid and the palatopterygoid arch.
4. Mode of articulation between upper jaw elements.
5. Similarities in the morphology of the vertebrae.

The diplospondylous condition of the centra in (presumably) near adult *Lycoptera* would seem to be more primitive than the monospondyly of *Hiodon*. Nelson (1969) considers the absence of the lower intermuscular bones a specialized feature. Since these bones are not developed in pholidophorids (Lund, 1966), nor in primitive teleosts like the leptolepids and ichthyodectids (including *Thrissops* and *Allothrissops*), I cannot agree with Nelson's conclusion.

Certain characters are less readily classified as primitive or derived. Among these perhaps should be included the infraorbital bones. Nelson (1969) suggests that the six infraorbitals in the Osteoglossomorpha (including *Hiodon*) probably represent a specialized condition *Lycoptera* seems to have the primitive number of seven (see page 270) but the elongate and slender lachrymal (1st infraorbital) is not typically that of the more primitive teleosts, and closely resembles the lachrymal of *Hiodon*. In these other fishes the lachrymal is stouter and deeper than in *Lycoptera* (see for example the figures of *Leptolepis* and *Thrissops* in Patterson [1967], and those of *Elops* and *Albula* in Nelson [1969, text fig. 7]). The infraorbitals of *Lycoptera* could well provide the basic type from which the *Hiodon* pattern evolved by the fusion of bones 3 and 4 (see Nelson, *op. cit.*) and the posterior extension of the 5th bone. The specialized condition of the *Lycoptera* antorbital is discussed above. The absence of a supraorbital bone in both *Hiodon* and *Lycoptera* is an unusual and probably a phyletically significant feature.

The reduced number of branchiostegal rays (*ca.* 8–10) in *Lycoptera* is certainly an advanced character. That this number is identical with the number occurring in *Hiodon*, and that both genera have the ceratohyal and branchiostegal rays of a similar shape, can I think be taken as evidence indicating relationship. A review of branchiostegal and ceratohyal shape in lower teleosts (including fossil taxa where this bone is preserved) brings to light no other species with branchiostegals and ceratohyal as similar to those of *Lycoptera* (personal observations, and McAllister, 1968). *Hiodon* has two hypophyals on each side (a primitive feature) but *Lycoptera* has only one (see page 272).

There is a marked similarity in the shape of the parasphenoid of *Lycoptera* and *Hiodon*, particularly with respect to the steep angle made between the orbital and occipital limbs of the bone. Such a sharply angled skull-floor is probably unique among primitive teleosts. The presence of a basipterygoid process on the parasphenoid of *Lycoptera* is, of course, a primitive feature lost in *Hiodon*.

Parapophyses fused with the vertebral centra is a specialized characteristic. In *Hiodon* the pleural ribs articulate with the centrum or with the parapophysis base where it is fused with the centrum. *Lycoptera*, although having fused parapophyses, retains the more primitive condition of ribs articulating with the tips of the parapophyses. It is noteworthy that in both *Hiodon* and *Lycoptera* the vertebral organization in general is primitive, yet the parapophyses are firmly fused with the centrum.

If my identification of the large otolith in *Lycoptera* as a lapillus is correct (see page 269), then there is a remarkable degree of similarity between the two genera in a most unusual specialization. Little is known about this otolith in lower teleosts, but no living elopomorph, osteoglossomorph or primitive euteleostean has a lapillus as like that of *Lycoptera* as is the lapillus of *Hiodon*.

There remain two characters, the caudal fin skeleton and the lateral temporal fenestra. These I consider to have great import in establishing a phyletic relationship between the lycopterids and hiodontids.

Although primitive characters persist in the caudal skeleton of *Hiodon* and *Eohiodon* (as for example a separate second ural centrum and seven hypurals) there are two other features which can only be considered derived ones. These are the single epural, and a reduction in the number of principal branched caudal rays to sixteen. In the primitive caudal fin there are three (rarely two) epurals, and seventeen branched rays (for further discussion see Greenwood and Patterson [1967], and Nelson [1969]). Another unusual feature, but one shared with some Mesozoic Ichthyodectidae (Patterson, 1968), is the arrangement of the uroneurals into a single series of elongate elements (see page 277).

In combination, the single uroneural series, the single epural, and the sixteen caudal rays of *Lycoptera* are otherwise found only in *Hiodon* and *Eohiodon*.

Likewise, a temporal fenestra bordered by the parietal, pterotic and epiotic is found only in *Lycoptera* and *Hiodon* (the condition in *Eohiodon* is unknown).

TAXONOMIC CONSIDERATIONS. On the basis of their shared specialized characters, I would conclude that the Lycopteridae are more closely related to the Hiodontidae than to any other group of teleosts. Several primitive features, lost in the Hiodontidae, are present in the Lycopteridae, which should therefore, be considered the plesiomorph sister group of the Hiodontidae.

In turn, the lycopterids and hiodontids together constitute a plesiomorph sister group to the more specialized Notopteridae. These relationships are perhaps best expressed by uniting the Hiodontidae and Lycopteridae in one superfamily (Hiodontoidea ; new taxon), and by creating another superfamily (Notopteroidea) for the Notopteridae. Both superfamilies can be included within the suborder Notopteroidei (order Osteoglossiformes) of Greenwood *et al*, 1966.

These conclusions are at variance with the opinions expressed by previous students of the Lycopteridae. Of these workers, five suggested (with varying degrees of confidence) relationship with the Cyprinidae (Cockerell [1925] ; Gregory [1933] ; Saito [1936] ; Takai [1944] ; Liu *et al* [1963]), three favoured affinity with the basal Clupeiformes *sensu* Berg (1940) (Berg [1948] ; Lehman [1966], Gaudant [1968]) and one, Yakovlev (1965), with the Osteoglossidae.

Evidence for relationship between the Lycopteridae and the Cyprinidae stems chiefly from similarity in scale morphology (Cockerell *op. cit.*) and from Reis' (1910) identification of the largest otolith as an asteriscus, thus implying a cyprinoid type of inner ear. However, no other anatomical or gross morphological features can be adduced to support this postulated relationship, and doubt can be thrown on the otolith evidence (see above, page 267). In all features generally thought to be important indicators of phyletic relationship (especially the caudal fin skeleton) the cyprinids and lycopterids are very distinct, and the same may be said for the other ostariophysan families (see Rosen and Greenwood, 1970).

A relationship between the Lycopteridae and certain basal teleosts (*i.e.*, the more primitive members of Berg's [1940] order Clupeiformes, such as the elopoids and leptolepoids) seems, at first sight, to be more reasonable. But again, apart from similarities in basic, primitive features the lycopterids differ in many important ways (caudal skeleton, number of branchiostegals, morphology and relative size of the otoliths, presence of a temporal fenestra, etc.) To classify the lycopterids with Berg's Clupeiformes would seem totally to disregard their phyletic affinities.

Yakovlev's (*op. cit.*) suggested relationship of *Lycoptera* with the osteoglossid *Arapaima* is of particular interest. However, the shared characters which Yakovlev lists are not critical ones ; most are primitive features found in all basal teleosts (a medioparietal skull, basipterygoid process on the parasphenoid, teeth on parasphenoid and basihyal plate). Of the others, I would doubt whether the nasals are contiguous in *Lycoptera* (see page 261), and a large opercular process occurs in other and unrelated lineages (see page 272). That *Lycoptera* is a member of the Osteoglossomorpha seems certain, but the nature of its caudal skeleton militates against its inclusion in the Osteoglossoidei (Greenwood, 1967 ; Nelson, 1969).

ZOOGEOGRAPHICAL IMPLICATIONS. Nelson (1969) has discussed at length evidence relating to the phyletic and geographical history of the Osteoglossomorpha. Important lacunae in this evidence concern the primary area of distribution, and the interrelationships, of the Hiodontidae. The lycopterid—hiodontid relationship proposed above does little to fill this gap except to strengthen the hypothesis that the hiodontid lineage was probably of north-eastern Asiatic origin. The problem of hiodontid–notopterid interrelations, and other aspects of osteoglossomorph geography will be reviewed in a forthcoming paper.

Weiler (in Martin and Weiler, 1954, 1957 and 1965) has referred a number of different otoliths, from the Mesozoic of Germany, to the suborder Lycopteroidei (*sensu* Berg, 1940). Like other authors, Weiler based his comparisons on Reis' (1910) figures. Even allowing for the difficulties inherent in this procedure, I cannot see a close resemblance between the German and Siberian otoliths ; none of the specimens figured by Weiler shows the characteristic outline and sculpturing of the larger otolith in *Lycoptera*. Thus, on the evidence of otoliths alone, it would by unwise to assume that lycopterid fishes occurred in Europe during the Mesozoic.

ACKNOWLEDGEMENTS

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SUMMARY

A comparative osteological study of the Mesozoic genus *Lycoptera* and members of the family Hiodontidae, indicates a close relationship between the two taxa. Of particular importance in this regard are the nature of the caudal fin skeleton, the number of caudal fin rays, the presence of a temporal fenestra, and details of the hyoid arch skeleton.

The peculiar otoliths of *Lycoptera* seem to resemble those of *Hiodon* and it is suggested that, contrary to earlier opinions, the inner ear of *Lycoptera* was probably of the *Hiodon*-type and not the cyprinid type.

Previous views on the relationships of the Lycopteridae are reviewed. No evidence can be found to support the idea that the Lycopteridae are ancestral cyprinids or that there is any relationship between the elopoid lineages and the Lycopteridae.

It is suggested that the Lycopteridae and Hiodontidae be placed in one superfamily, the Hiodontoidea, and that the apomorph sister group of this taxon is the superfamily Notopteroidea (containing only the Notopteridae).

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A REDESCRIPTION OF THE SPECIES OF *EUPOLYBOTHRUS* VERHOEFF S.STR.

PRESERVED IN THE BRITISH MUSEUM (NATURAL HISTORY) AND THE HOPE DEPARTMENT OF ZOOLOGY, OXFORD (CHILOPODA, LITHOBIOMORPHA)

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20 JUL 1970
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A REDESCRIPTION OF THE SPECIES OF *EUPOLYBOTHRUS* VERHOEFF S. STR.

BY E. H. EASON

SYNOPSIS

Lithobius fasciatus Newport has long been regarded as the senior synonym of *Lithobius grossipes* C. L. Koch, a widespread Alpine species. *Lithobius litoralis* L. Koch, hitherto known only from its original description, is another previously accepted synonym. The type material belonging to these three species has been critically examined; they are fully redescribed and are shown to be three distinct species of the subgenus *Eupolybothrus* Verhoeff s.str. *Lithobius fasciatus graecus* Verhoeff is redescribed; it is regarded as a subspecies of *Eupolybothrus litoralis*.

INTRODUCTION

Chamberlin (1925) designated *Lithobius grossipes* C. L. Koch as the generotype of *Eupolybothrus* Verhoeff (1907) and the nominate subgenus, as emended by Jeekel (1967), contains this species which was previously known as *E. fasciatus* (Newport), and its close relatives. Although the latter comprise a large number of nominal species, subspecies and varieties, most of these are based on scanty descriptions of inadequate material and depend for their definition on unstable characters of little taxonomic importance. Many of these forms will undoubtedly prove to be identical with one another and the subgenus is in need of revision.

The material belonging to *Eupolybothrus* s. str. in the British Museum (Natural History) and the Hope Department of Zoology is referable to three species, *E. fasciatus* (Newport), *E. grossipes* (C. L. Koch) and *E. litoralis* (L. Koch) and includes the type specimens of each of them. The conclusions to be drawn as to their identity are quite different to those previously accepted and it therefore seems desirable, pending a thorough revision of the subgenus, to describe these three species in detail from the above material, particularly as they are likely to prove to be the predominant surface-dwelling species of the subgenus, and indeed of the genus, in southern Europe and the Balkans.

TAXONOMIC CHARACTERS

In order to separate the three species under review the following features of the legs are of special importance.

Chaetotaxy

In addition to the general setae irregularly disposed on all the articles there are, on the ventral aspects of the tarsi and metatarsi, clearly differentiated somewhat decumbent setae arranged in linear series parallel to the long axis of the article. These series of setae have been called "pectines" by Crabill (1958) who uses their arrangement on the first 13 legs to differentiate between American species of *Eulithobius* ;

although they are also evident on the first 13 or 14 legs of many of the larger species of *Lithobius* they have not attracted much attention from European workers. In the present species of *Eupolybothrus* there are two such series on each of the tarsi and metatarsi of the 13th and more anterior legs, one or two on the 14th metatarsus and one on the 14th tarsus; they are not found on the 15th tarsus but on the 15th metatarsus a single series may or may not be present according to species.

These seriate setae are only a little stouter than the general setae but at the distal end of the ventral aspect of the 14th tarsus and in a similar position on the tarsi and tibiae of the 13th and more anterior legs are usually found stout spinous setae, easily mistaken for small spines in the positions VaTa, VpTa and VpT; those on the 14th tarsus differ in arrangement in each species. Since the general setae of the 14th and 15th legs also show marked interspecific variation there are three distinct kinds of setae, general, seriate and spinous, all of which are useful in separating the species. Finally, mature males usually bear a distinctive tuft of setae on the internal basal angle of the 15th femur.

Sculpturing of male 15th legs

Although there are one or two longitudinal dorsal sulci on the prefemur, femur and tibia of each of the 14th and 15th legs in both sexes, only the sculpturing of the adult male 15th femur is really distinctive. On this article much of the dorsum of the base is occupied by a pit, continuous with the internal dorsal sulcus. On the internal aspect of the distal end of the article is an area of greater or lesser extent which is clearly demarcated from the rest of the shaft by being free of glandular pores and of a rather paler colour; this is the "pore-free area" of Chamberlin (1952 : 212) and may bear special features such as a swelling, a concentration of setae or a small circumscribed group of very fine pores corresponding to the "fine pore-sieve" of Chamberlin (1952 : 214).

REDESCRIPTIONS

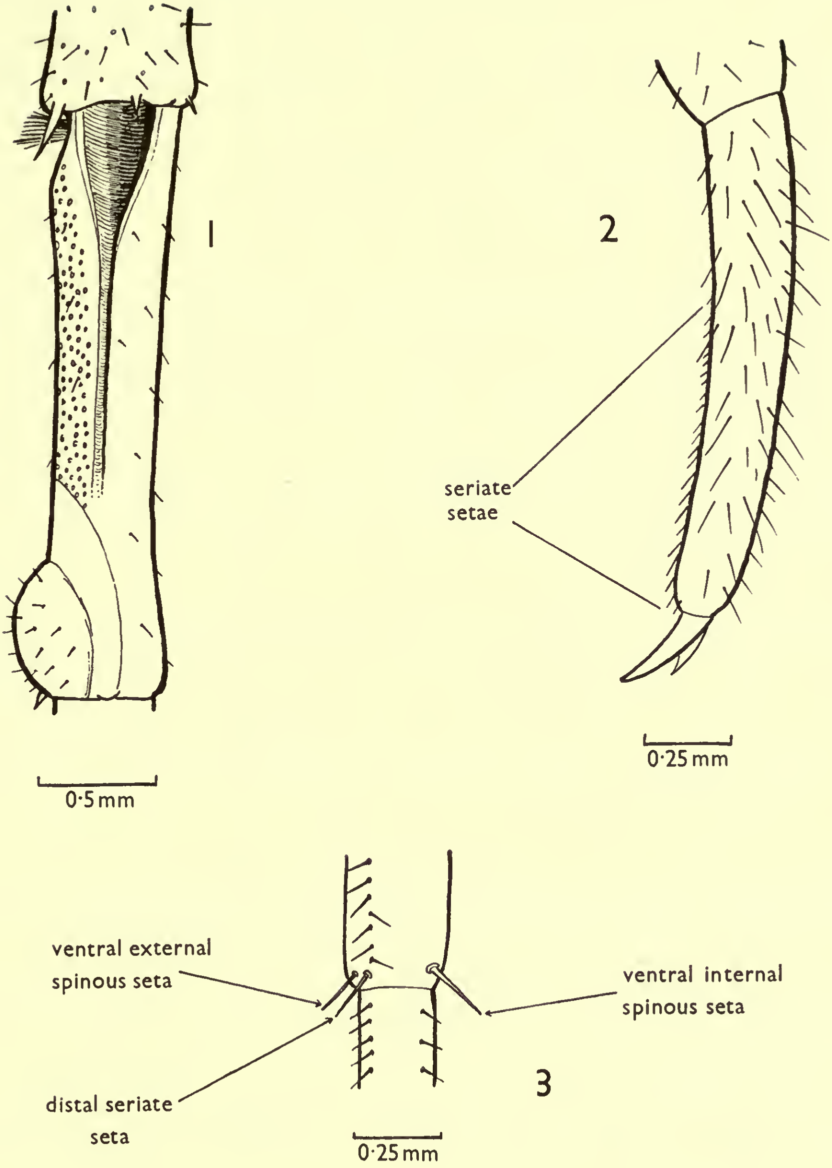
Eupolybothrus (E.) fasciatus (Newport)

Figs. 1 to 3

Lithiobius fasciatus Newport, 1844, p. 365.
Lithobius (*Polybothrus*) *fasciatus bosniensis*: Verhoeff, 1900, p. 162.
not *Lithobius fasciatus* Muralewitsch, 1929, p. 102.

MATERIAL EXAMINED. Three dried specimens in a fair state of preservation, all males, are present in the Newport Collection of Myriapoda in the Hope Department of Zoology, Oxford. I have designated these specimens A, B and C. Specimen A, 23 mm long, is pinned through the 5th tergite and lacks the 14th and 15th legs; it bears a label "Lithobius fasciatus Newp." but no indication of locality. Specimens B and C, though unlabelled, are arranged in the cabinet immediately on either side of specimen A. Specimen B, 23 mm long, is pinned through the 7th tergite and has the 14th and 15th legs intact on the right side only. Specimen C, 22 mm long, is pinned through the 6th tergite and lacks the 14th and 15th legs.

Although much of the original description of this species is based on specimens up


1
0·5 mm
2
seriate setae
0·25 mm
ventral external spinous seta
distal seriate seta
ventral internal spinous seta
3
0·25 mm

FIGS. 1 to 3. *Eupolybothrus fasciatus.* 1. Femur and distal part of prefemur of 15th leg (dorsal view). 2. Metatarsus of 15th leg (external view). 3. Region of tarso-metatarsal articulation of 14th leg to show seriate and spinous setae (ventral view). All figures taken from Newport's specimen B (♂ 23 mm. long) to 32 mm long with 9+9 prosternal teeth, Newport (1844) states that his material was deposited in the Hope Museum and careful comparison of the writing on the label attached to specimen A with an example of Newport's handwriting in the Sherborne Collection of Manuscripts in the British Museum (Natural History) leaves little doubt that the label is, in fact, in Newport's hand. These three specimens, therefore, seem to be the only survivors of the syntypical series. Specimen A, bearing the label, should be regarded as the lectotype but we must depend for the characters of the 14th and 15th legs on specimen B.

The following specimens, preserved in spirit, are present in the Koch Collection of Arachnida and Myriapoda in the British Museum (Natural History) and are labelled "grossipes, Rom" in L. Koch's hand (Reg. no. 13. 6. 18. 301–302) :

A male 22 mm long lacking the 14th and 15th legs and a female 23 mm long.

The following specimens, preserved in spirit, are present in the Verhoeff Collection of Myriapoda in the British Museum (Natural History) and are labelled "Lithobius fasciatus bosniensis Latz." "Bosnia" (Reg. no. 03. 8. 25. 41–46) :

A well-preserved male 27 mm long, a mutilated male 24 mm long lacking most of the legs and four females 23 to 26 mm long.

It seems reasonable to assume that these specimens were among those on which Verhoeff (1900 : 162) based his records of *L. fasciatus bosniensis* from Bosnia (Yugoslavia).

DIAGNOSIS OF ADULT. Length 22 to 32 mm. Antennae of 36 to 42 articles. Glandular pores of 15th leg concentrated on internal aspects of femur, tibia, tarsus and metatarsus only. 15th metatarsal general setae up to three-quarters the diameter of the article in length. 15th metatarsal seriate setae present. Basal pit of male 15th femur extensive and deep. Internal dorsal sulcus of male 15th femur not extending to margin of pore-free area which bears a prominent globular swelling. No coxolateral spines.

DESCRIPTION OF ADULT. *Length*: present specimens from 22 to 27 mm (Newport gives 1¼ inches = 32 mm) ; 15th legs about half body-length. *Colour* : Newport's dried specimens vary from pale (specimen A) to dark (specimens B and C) brown ; those preserved in spirit are intermediate in colour with a trace of a darker dorsal median band. *Antennae* : about half body-length ; of 36 to 42 articles, the distal 12 or so often elongate. *Ocelli*: 1+4, 5, 4, 1 ; 1+4, 3, 4, 3 ; 1+4, 4, 5, 4, 3 etc.; those of the superior row horizontally oval, widely spaced and larger than those of the other rows ; posterior superior ocellus almost as large as isolated posterior ocellus. *Prosternum* : with 6+6 to 9+9 small teeth : lateral spines variable in structure and position, usually peg-like but sometimes dentiform or setiform and often of different structure on either side of the same individual, usually placed well lateral to the external teeth but sometimes immediately postero-lateral or rarely postero-medial. A specimen from Rome has 10+7 teeth, possibly due to abnormal development. *Tergites* : posterior borders of large tergites slightly emarginate ; posterior angles of T.5 rounded, those of T.8 blunt without angulation, those of T.10 somewhat angulated, those of T.12 and 14 distinctly angulated but without projections ; posterior angles of T.4 rounded without trace of projections ; posterior projections on T.6 rounded, those on T.7 short and broad, those on T.9, 11 and 13 well-developed with internal borders very slightly sinuous ; posterior border of intermediate tergite sinuous in male, with rounded or trapezoidal emargination in female. *Coxal pores* : from 15 in smaller specimens to 35 in larger specimens, in about four rows on each of the 12th to 15th coxae. *Glandular pores of 15th legs* (Fig. 1) : concentrated on internal aspects only of femur, tibia, tarsus and metatarsus. On the femur the pores are limited by the internal dorsal sulcus ; on the prefemur they are sparse as figured by Verhoeff (1937 : 172, fig. 1) for *Polybothrus apenninigenus*.

Chaetotaxy of 14th and 15th legs

General setae : on the metatarsus numerous, up to three-quarters the diameter of the article in length (Fig. 2) ; of much the same density and absolute length on the tarsus, about a quarter the diameter of the article in length ; on the tibia and femur (Fig. 1) sparser and rather shorter ; on the prefemur rather denser, longer and stouter than on tibia or femur, particularly along the ventral aspect of the article. *Seriate setae* : a single row on the distal half to three-quarters of the 15th metatarsus (Fig. 2), a well-defined external row and a rather sparse internal row along the length of the 14th metatarsus and a single row on the distal half to three-quarters of the 14th tarsus (Fig. 3). *Spinous setae* : on the 14th tarsus the distal seriate seta and the ventral external seta (VaTa) are of much the same size, rather stouter than the other seriate setae, while the ventral internal seta (VpTa) is much stouter (Fig. 3). *Setae of tuft* (males) : long and numerous in Newport's specimen B (Fig. 1) ; absent in Verhoeff's specimen.

Sculpturing of male 15th legs (Fig. 1)

These characters are taken from the right leg of Newport's specimen B and both legs of Verhoeff's larger male : prefemur with internal dorsal sulcus distinct on right leg of Verhoeff's specimen only, otherwise faint, no external sulcus ; basal femoral pit deep and extensive, occupying about three-quarters the diameter of the base of femur, rather sharply attenuated distally, continuous with the fairly broad internal femoral sulcus which becomes gradually shallower distally to disappear before reaching the margin of the pore-free area ; external femoral sulcus absent ; pore-free area occupying distal one third of the internal aspect of femur, bearing a prominent globular swelling on which the general setae are of the same structure as those on the rest of the shaft but a little denser ; on the right leg of Verhoeff's specimen is a well-circumscribed slightly raised oblong fine pore-sieve at the centre of the globular swelling about a quarter the diameter of the distal end of the femur, bearing a rather ill-defined tuft of minute setae ; on the left leg of the same specimen only a small faint group of fine pores can be seen on the surface of the globular swelling whereas in Newport's specimen B this character was not confirmed, possibly being obscured by the slight shrivelling of the integument which tends to occur in dried material.

Sculpturing of male 14th legs

Internal and external dorsal sulci distinct on both prefemur and femur.

Spinulation

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	—	m	amp	amp	am	a	—	amp	a–p	a–p
15	—	m	amp	amp	am	a	—	amp	p	p

15 VpF may be absent ; no coxolateral spines ; a well-developed 15th accessory apical claw.

Genitalia

Male : posterior border of genital sternite with a median notch and marginal setae showing no obvious differentiation ; gonopods long and slender, basal article less than half the length of distal article. *Female* : two cylindro-conical spurs on each gonopod, separated from one another at their insertion by rather more than their own diameter ; claw of gonopod sharp, without denticles ; dorso-lateral setae of gonopod short, in an irregular band of about five setae on the first article, about twelve on the second and none on the terminal article.

DISCUSSION. Latzel (1880) suspected *Lithobius fasciatus* Newport of being the same as *Lithobius grossipes* C. L. Koch and in his paper on Ligurian centipedes Pocock (1890), after examining the type material of *L. fasciatus* in the Hope Museum, says definitely that these two species are identical. Ever since, *L. fasciatus* has been regarded as the senior synonym of *L. grossipes*. But it is now clear that Newport's specimens are distinct, not only from the holotype of *L. grossipes* and most of the other specimens in the Koch Collection assigned by L. Koch to this species, but also from the Ligurian specimens on which Pocock presumably based his conclusion (see p. 297).

Newport (1844) gives Florence and Naples as the type localities of *L. fasciatus*, mentioning that specimens from Naples are usually of a much lighter colour than those from Florence. If we assume that specimen A, which is markedly paler than either B or C, comes from Naples and that specimens B and C come from Florence it is just possible, since the two species are very hard to separate without reference to the structure of their 15th legs, that specimen A belongs to *Eupolybothrus grossipes* and that Pocock examined it before its 15th legs were lost, omitted to examine specimens B and C, and came to the correct conclusion. But Newport states that specimens from the two localities agree with one another precisely except in their colour and he describes the "metatarsal joints" of the posterior legs as "very hairy" which he would hardly have done had his specimens included mature examples of *E. grossipes*. It therefore seems reasonable to regard Newport's three specimens as conspecific.

The difference between these specimens and those referred by Verhoeff to *L. fasciatus bosniensis* seems only to be due to individual variation. Colour is altogether unreliable as a taxonomic character and, in any case, dried specimens and those preserved in spirit are not comparable with one another in this respect. The prominent tuft of setae on the internal basal angle of the male 15th femur, absent in Verhoeff's specimen, was noted by Latzel (1888) in his original description of *bosniensis* but

Attems (1902) remarks on its absence in some specimens. It seems that these setae, which are absent from all but the fully mature examples of *E. grossipes* and *E. litoralis* that I have examined, may fail to appear even in the adult.

There is therefore little doubt that Verhoeff's specimens are indeed identical with *L. grossipes* var. *bosniensis* Latzel (1888) and this form, originally recorded from a number of localities in Bosnia and Hercegovina, will almost certainly prove to be identical with *E. fasciatus* and was only named because Latzel was unfamiliar with Newport's species. The same may be said of *L. fasciatus* var. *apenninigenus* Brolemann (1894), originally recorded from Borgotaro in the northern Apennines, which agrees with Latzel's rather scanty original description and only differs from Attems (1902) expanded redescription of *bosniensis* in quite unimportant characters. It is also safe to assume that Verhoeff (1934 and 1937) had specimens of *E. fasciatus* before him when he wrote his descriptions of *Polybothrus apenninigenus.*

The labelling of specimens of *E. fasciatus* as "grossipes" by L. Koch is hardly surprising as the characters separating these two species are unlikely to have attracted his attention.

Eupolybothrus (E.) grossipes (C. L. Koch)

Figs. 4 to 7

Lithobius grossipes C. L. Koch, 1847, p. 146; L. Koch, 1862, p. 32, fig. 4.
Lithobius montanus C. L. Koch, 1847, p. 148; L. Koch, 1862, p. 27, fig. 1.
Lithobius festivus L. Koch, 1862, p. 29, fig. 2.
Lithobius (*Eulithobius*) *fasciatus*: Pocock, 1890, p. 61.

MATERIAL EXAMINED. The following specimens, preserved in spirit, are present in the Koch Collection of Arachnida and Myriapoda in the British Museum (Natural History) ; except where otherwise stated the labels appear to be in L. Koch's hand :

"Lithobius grossipes C. Koch, festivus L. Koch" "Idria" (Reg. no. 13.6.18. 262).

This specimen, a female 30 mm long, although preserved in spirit has obviously been dried. An unusual feature is that the 14th leg appears stouter than the 15th ; this appearance was noted, not only by L. Koch (1862) who undoubtedly used this specimen for his description of *L. grossipes*, but also by C. L. Koch (1847) in his original description. I therefore believe it to be the holotype and have labelled it accordingly. The fact that C. L. Koch gives Trieste as the type locality is consistent with the same specimen having been used for both descriptions since Idria (Idrija, Yugoslavia) is in the neighbourhood of Trieste.

"Lithobius grossipes C. K." "Hopfgarten, 26 August, 1868" (Reg. no. 13.6.18. 263–265).

Three females 28 to 30 mm long.

"Lithobius grossipes C.K." "Seiseralpe [an alpine hut in Italy], *[*leg.*] Gredler" (Reg. no. 13.6.18. 266).

This specimen, a male 35 mm long, agrees in detail with L. Koch's (1862) description of *L. montanus* C. L. Koch, a description based on a single specimen sent him

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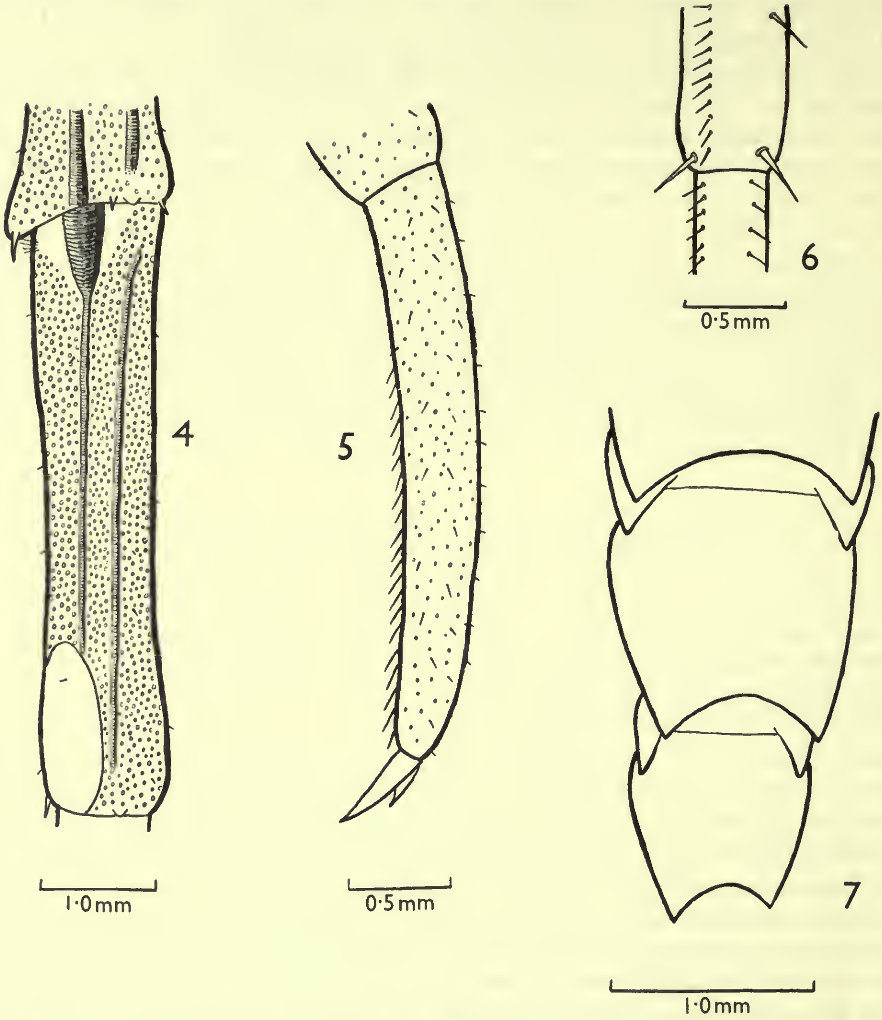
* Words in brackets throughout this paper are the author's additions to the original labels.



Figs. 4 to 7. *Eupolybothrus grossipes*. 4. Femur and distal part of prefemur of 15th leg (dorsal view). 5. Metatarsus of 15th leg (external view). 6. Region of tarso-metatarsal articulation of 14th leg to show seriate and spinous setae (ventral view). 7. 11th to 14th tergites (dorsal view). Figs. 4 to 6 taken from a ♂ from Busalla (43 mm long); fig. 7 taken from a stadium agenitalis 1 from Busalla (10 mm long).

by Prof. P. Gredler from "Seiseralpe" in South Tyrol. This is undoubtedly the specimen in question and was presumably relabelled by L. Koch when he realised its identity with *L. grossipes*, of which *L. montanus* is now an accepted synonym.

"grossipes, Eisarkthal [Valle dell'Isarco, Italy] 1870" (Reg. no. 13. 6.18. 267–269). Two females and a male 30 to 31 mm long.

"Lithobius grossipes C.K., festivus L.K." "Sudtirol" (Reg. no. 13.6.18. 270–282, part).

Two females 35 and 37 mm long, a mature male 34 mm long and two immature females 17 and 21 mm long.

"grossipes, Sudtirol" (Reg. no. 13.6.18. 270–282, part).

A single female 37 mm long.

"Lithobius grossipes C.K., festivus L.K." "Sudtirol" (Reg. no. 13.6.18. 270–282, part).

Four mature females 28 to 31 mm long and three immature females 16 to 21 mm long.

"Lithobius grossipes C.K., festivus L.K." "Sudtirol" (Reg. no. 13.6.18. 270–282, part).

Three mature males 28 mm long and two immature males 12 and 14 mm long.

"Lithobius grossipes C. Koch." "Meran [Merano, Italy], [*leg.*] Milde" (Reg. no. 13.6.18. 283–292, part).

Three females 27 to 30 mm long, six mature males 27 to 38 mm long and an immature male 19 mm long.

"grossipes, Meran [Merano, Italy], [*leg.*] Ausserer" (Reg. no. 13.6.18. 283–292, part).

An immature male 23 mm long.

"Lithobius grossipes C.K." "Garmisch" (Reg. no. 13.6.18. 293).

An immature male 24 mm long. Although not agreeing in every detail with L. Koch's (1862) original description of *L. festivus* from Garmisch (Bavaria) this may be one of the specimens on which it was based.

"grossipes, Ballino [Italy] 12.IX.69" (Reg. no. 13.6.18. 298).

An immature female 17 mm long. The identity of this specimen is doubtful ; it may possibly belong to *E. fasciatus*.

"L. grossipes." "Susa, Oberitalien" (Reg. no. 13.6.18. 299–300).

Two immature males 18 and 24 mm long. The locality label is in L. Koch's hand but the identity label has been rewritten.

"leptopus? Hopfgarten" (Reg. no. 13.6.18. 365).

An immature female 13 mm long.

The following specimens are in the British Museum (Natural History), preserved in spirit in a jar labelled "Lithobius fasciatus Newp. Liguria, O. Thomas" in Pocock's hand (Reg. no. 89.3.8. 1–2) :

A total of 31 specimens ranging in size from fourth larval stadia 9 mm long to a mature male 43 mm long. These specimens almost certainly come from Busalla (Liguria, Italy) both because Pocock (1890) mentions Busalla as the locality and Mr. Oldfield Thomas as the collector of examples of "*L. fasciatus*" in his paper on Ligurian centipedes, and because they were mixed with two specimens of *Lithobius doriae* Pocock ; in the same paper this author describes *L. doriae* as a new species not only from the same locality (Busalla) but also from the same habitat as "*L. fasciatus*" (Pocock, 1890 : 59 & 64) and he must mistakenly have included specimens of the two species under the same label. I have relabelled these two examples of *L. doriae* and placed them in a separate tube.

The following specimens were contained in the above jar along with the Ligurian specimens but in separate tubes :

A badly mutilated " stadium agenitalis " 12 mm long labelled " Eulith. grossipes, Grande Chartreuse [Isère, France], [*leg.*] A. Dollfus " (Reg. no. 89.3.10. 1, part) and a badly mutilated immature male 15 mm long labelled " L. grossipes Koch, Portofino [Italy] " (Reg. no. 89.3.10. 1, part). Both labels appear to be in Pocock's hand ; in neither case is it possible to identify the specimens other than as species of the subgenus *Eupolybothrus.*

DIAGNOSIS OF ADULT. Length 27 to 43 mm. Antennae of 40 to 58 articles. Glandular pores of 15th leg concentrated on internal and dorsal aspects of prefemur and all aspects of other articles. 15th metatarsal general setae rarely exceeding a quarter the diameter of the article in length. 15th metatarsal seriate setae present. Basal pit of male 15th femur small and shallow. Internal dorsal sulcus of male 15th femur extending to margin of pore-free area which is not swollen. No coxolateral spines.

DESCRIPTION OF ADULT. *Length* : 27 to 43 mm ; 15th legs up to two-thirds of body-length. *Colour* : pale to dark brown, often with a darker dorsal median band. *Antennae* : half to two-thirds of body-length, sometimes shorter in female ; of 40 to 50 (female) and 47 to 58 (male) articles, the distal 10 to 14 often very elongate in large specimens. *Ocelli* : number and general pattern as described for *E. fasciatus* ; in some specimens, however, the ocelli of the superior row may be round rather than oval and little larger than the others, but they are always relatively widely separated from one another. There is a tendency for the ocelli of the second, third and fourth rows to be more numerous than those of the superior row but this is by no means invariable. *Prosternum* : with 6+7 to 8+9 small teeth, usually 7+7 or 8+8 ; minute setiform lateral spines immediately postero-lateral to the external teeth in some specimens, but these spines are often absent from one of both sides, particularly in large specimens, possibly due to damage. *Tergites* : emargination of posterior borders of large tergites variable, particularly that of T.14 which may be quite markedly emarginate or may be almost straight ; posterior angles of T.5 rounded or blunt, those of T.8 blunt or angulated sometimes with traces of projections, those of T.10 blunt or angulated often with slight projections, those of T.12 sometimes blunt but usually angulated with slight projections, those of T.14 blunt or angulated, sometimes rounded ; posterior angles of T.4 usually rounded, sometimes very slightly projecting. Posterior projections on T.6 always well-developed, usually blunt, sometimes sharp ; those on T.7 well-developed, sometimes very broad and short, with or without some sinuosity of their internal borders ; those on T.9, 11 and 13 well-developed with internal borders more or less sinuous ; in some specimens this sinuosity is so marked, particularly on T.11 and 13, that the tip of the projection is narrow and pointed as in the figured immature female of *E. litoralis* (Fig. 12). Posterior border of intermediate tergite sinuous in male, with rounded or trapezoidal emargination in female. *Coxal pores* : 35 to 65 in four to six irregular rows on each of the 12th to 15th coxae, most numerous on 14th. *Glandular pores of 15th legs* (Fig. 4) : concentrated on all aspects of femur, tibia, tarsus and metatarsus, and also on internal and dorsal aspects of prefemur as figured by Verhoeff (1937 : 172, fig. 2) for "*Polybothrus fasciatus*".

Chaetotaxy of 14th and 15th legs

General setae : on the metatarsus sparse and short, not more than a quarter the diameter of the article in length, usually much less in males (Fig. 5), sometimes a little longer in females ; on the tarsus, tibia, femur (Fig. 4) and prefemur shorter and sparser than on metatarsus, sometimes a little longer in females than in males. *Seriate setae* (Figs. 5 & 6) : as in *E. fasciatus*, but in females those of the 15th metatarsus may be reduced to about three at the distal extremity of the article. *Spinous setae* : on the 14th tarsus the ventral external and ventral internal setae are of much the same structure (Fig. 6) and correspond to the "spines" VaTa and VpTa described by Brolemann (1930 : 246) in "*Bothropolys fasciatus*" ; in addition to the ventral internal seta there are, in large specimens, a few more spinous setae at intervals along the ventro-internal border of the tarsus. On the 13th and more anterior legs the spinous tarsal setae are similar to those on the 14th but rather more numerous along the ventro-internal border ; the tibia of each of these legs also bears a linear series of spinous ventro-internal setae, the most distal of which corresponds to the "spine" VpT of Brolemann. *Setae of tuft* (males) : short and few, but present in all adults examined (Fig. 4)

Sculpturing of male 15th legs (Fig. 4)

Prefemur with dorsal sulci distinct, internal one continuous with basal femoral pit, external one not reaching the distal end of article ; basal femoral pit shallow, occupying about a quarter to a third the diameter of the base of femur, continuous distally with the narrow internal femoral sulcus which runs to the margin of the pore-free area and is of the same width and depth throughout ; external femoral sulcus similar in width, starting level with the basal pit and extending further distally than the internal sulcus ; pore-free area occupying distal one third or less of the internal aspect of femur, with no swelling, almost glabrous, the minute setae on its surface being just as sparse as on the rest of shaft.

Sculpturing of male 14th legs

Internal and external dorsal sulci usually fairly distinct on both prefemur and femur.

The 14th leg of holotype

The femur (R. only) is unusually broad so that the 14th leg appears stouter than the 15th ; this appearance is not due to defective development of the 15th leg as suggested by Latzel (1880 : 48).

Spinulation

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	—	m	amp	amp	am	a	—	amp	a–p	a–p
15	—	m	amp	am	am	a	—	amp	p	p

14 VpF and 15 DpT may be absent ; 15 VpF and 15 DaF may be present ; no coxolateral spines ; a well-developed 15th accessory apical claw.

Genitalia.

Male : posterior border of genital sternite with a median notch, more distinct in large specimens, and long marginal setae on either side, the medial setae adjacent to the notch being often shorter than the more lateral setae but showing no sharp differentiation ; gonopods long and slender, basal article less than half the length of distal article. *Female* : two cylindro-conical spurs on each gonopod separated from one another at their insertion by about their own diameter, the internal pair being often rather smaller than the external pair even in mature specimens ; claw of gonopod sharp, without denticles ; dorso-lateral setae of gonopod short and stout, in an irregular band of about six setae on the first article, about twelve on the second and none on the terminal article. In large specimens the spurs of the gonopods may be short and blunt and the claw blunt, possibily due to wear and tear.

IMMATURE STADIA. There is sufficient available material to describe the last larval stadium and five further stadia which probably cover the complete post-larval life-history. It is difficult to make an exact comparison between each of these stadia and those described by Verhoeff (1905) for *Lithobius forficatus* ; Verhoeff's terms are only roughly applicable and are therefore placed in parenthesis.

Fourth larval stadium

Length : about 9 mm. *Antennae* : 19 to 24 articles. *Prosternal teeth* : usually 6+6, sometimes 6+5 or 6+4. *Tergites* : posterior border of last tergite (T.12) deeply emarginate ; posterior projection on T.6, 7, 9 and 11 well-developed. *Coxal pores* : one on 12th coxa.

First post-larval stadium (agenitalis 1)

Length : about 10 mm. *Antennae* : broken. *Ocelli* : 1+2, 1. *Prosternal teeth* : 6+6 or 6+7. *Tergites* (Fig. 7) : posterior borders of large tergites deeply emarginate ; posterior projections on short tergites well-developed and much narrower than in adults. *Coxal pores* : 2, 2, 2, 1. *14th and 15th legs* : missing.

Second post-larval stadium (agenitalis 2)

Length : about 12 mm. *Antennae* : broken. *Ocelli* : 1+2, 2. *Prosternal teeth* : 6+6 or 6+7. *Tergites* : as in last stadium. *Coxal pores* : one relatively large external pore and 4 to 6 much smaller pores on each of the 12th to 15th coxae. *14th and 15th legs* : missing. *Genitalia* : undeveloped.

Third post-larval stadium (immaturus)

Length : 12 to 14 mm. *Antennae* : 38 articles. *Ocelli* : 1+3, 3, 2. *Prosternal teeth* : 6+6 to 7+7. *Tergites* : posterior borders of large tergites as in last stadium ; posterior projections on short tergites rather less narrow ; posterior border of intermediate tergite straight. *Coxal pores* : 7 to 10 on each of the 12th to 15th coxae. *General setae of 14th leg* : those of metatarsus exceeding the diameter of the article in length. *Seriate setae of 14th leg* : as in adult. *Spinous setae of 14th leg* : not fully developed. *Spinulation of 14th legs* : as in adult. *15th legs* : missing. *Male genitalia* : posterior border of genital sternite without a notch, with or without one or two marginal setae on either side ; gonopods appears as unsegmented slender buds. *Female genitalia* : gonopods small with indefinite segmentation and neither spurs nor claw.

Fourth post-larval stadium (*praematurus*)

Length : 15 to 18 mm. *Antennae* : 39 or 40 articles. *Ocelli* : 1+3, 3, 3 or 1+3, 3, 2, 2. *Prosternal teeth* 6+6 to 7+7. *Tergites* : approaching the shape found in adults, but posterior borders of large tergites tend to be more deeply emarginate and posterior projections on short tergites tend to be narrower and sharper ; posterior border of intermediate tergite straight or slightly emarginate in either sex. *Coxal pores* : 10 to 19 on each of the 12th to 15th coxae, usually many more on 12th than on 15th. *Glandular pores of 15th legs* : as in adult. *General setae of 14th and 15th legs* : much longer than in adult, those of metatarsus being about as long as the diameter of the article. *Seriate setae of 14th and 15th legs* : those of 14th tarsus and metatarsus as in adult ; those of 15th metatarsus reduced to a few at the distal extremity of the article. *Spinous setae of 14th leg* : not fully developed. *Setae of tuft* (male) : absent. *Sculpturing of 15th legs* : indistinct in males as in females. *Spinulation of 14th and 15th legs* : as in adult. *Male genitalia* : posterior border of genital sternite with or without a trace of median notch, with about 3 or 4 marginal setae on either side ; basal article of gonopod as long as distal article. *Female genitalia* : gonopods fairly well-developed, completely segmented, with or without minute spurs, with a small claw.

Fifth post-larval stadium (*pseudomaturus*)

Length : 19 to 25 mm. *Antennae* : 40 to 49 articles. *Ocelli* : 1+3, 4, 3 to 1+4, 4, 3, 2. *Prosternal teeth* : 7+7 to 8+9. *Tergites* : as in last stadium but posterior border of intermediate tergite very slightly sinuous in male, with rounded or trapezoidal emargination in female. *Coxal pores* : 20 to 35 on each of the 12th to 15th coxae. *General setae of 14th and 15th legs* : those of metatarsus up to half and those of tarsus up to one third of the diameter of the article in length ; others relatively shorter than in last stadium but longer than in adult. *Seriate setae of 14th and 15th legs* : as in adult but sometimes slightly reduced on 15th metatarsus. *Spinous setae of 14th leg* : as in adult, or the ventral external seta more slender. *Setae of tuft* (male) : absent. *Sculpturing of 15th legs* : femoral sulci more distinct in males than in females, but basal femoral pit and pore-free area absent or ill-defined. *Male genitalia* : posterior border of genital sternite usually with a feeble median notch and about 6 to 8 marginal setae on either side ; basal article of gonopod about half the length of distal article. *Female genitalia* : gonopods with small unequal spurs and a well-developed claw.

DISCUSSION. This is the species which, ever since the publication of Pocock's (1890) synonymy (see p. 294), has been regarded by most authors as the typical form of *Lithiobius fasciatus* Newport. But Chamberlain (1925) designated *L. grossipes* C. L. Koch as the type species of *Eupolybothrus* and only he, among modern authors, uses

C. L. Koch's name either because he was not familiar with the current European literature or because he regarded Newport's description of *L. fasciatus* as inadequate.

It seems that when L. Koch redescribed *L. grossipes* in 1862 he had only the holotype before him and identified his other available specimens of the species either as *L. montanus* C. L. Koch or as a new species, *L. festivus*, based on immature examples. Most of the material in the Koch Collection was probably named subsequent to 1862 when L. Koch must have realised the identity of these three forms with one another and labelled them "L. grossipes" of "L. grossipes, festivus." His reason for the continued use of the name " festivus " on some of the labels is quite obscure and was not based on immaturity.

E. grossipes has been fairly adequately described under either *grossipes* or " *fasciatus* " by a number of authors. Verhoeff (1937 : 178) describes T.8, 10, 12 and 14 as having rounded posterior angles and T.9, 11 and 13 as having posterior projections with almost rectilinear borders. Whereas a few of Koch's specimens have rounded angles on the large tergites as figured by Verhoeff (1937 : 174, fig. 7, oben) for "*fasciatus* ", the majority of Koch's and all Pocock's specimens have sharp or even slightly produced angles, particularly on T.10 and 12, much as figured by Verhoeff (1937 : 174, fig. 7, unten) for *Polybothrus baldensis*. The posterior projections on the short tergites are more often as described and figured by Verhoeff (1937 : 173, fig. 6) for " *fasciatus* " but there is considerable variation and those of T.11 and 13 may have their internal borders so sinuous and emarginate, and their extremities so narrow, that they resemble the figure of *E. litoralis* (Fig. 12) or even Verhoeff's (1937 : 173, fig. 4) figure of T.13 in *P. baldensis*. The exact shape of the trunk tergites is so variable that it is of little use as a taxonomic character, and the above description as well as the figures of *E. litoralis* (Figs. 10 & 12) might apply equally to each of the three species under consideration.

But this tendancy of the tergites to differ from the shape described by Verhoeff for " *fasciatus* " does occur more often in immature specimens both as regards the narrowing of the projections on the short tergites and the sharper angulation of the large ones ; sharper angulation of the latter is often associated with increased concavity or emargination of their posterior borders as described by Verhoeff (1934 : 72) for *Polybothrus fasciatus albanicus*. Verhoeff's statement, therefore, when describing *albanicus*, that tergal projections are weaker (blunter) in immature than in mature specimens is not true of *E. grossipes* although it may be true of many species of Lithobiidae. These variations are well shown by Pocock's specimens, the majority of which are immature. For example, angulation and emargination of T.14 is most marked in the earliest post-larval stadium (Fig. 7) and the last tergite (T.12) of the fourth larval stadium is even more deeply emarginate.

Although in mature males the seriate setae of the 15th metatarsus are extensive (Fig. 5) and the general setae of this and other articles of the 14th and 15th legs are very short, in immature specimens (and sometimes in mature females) the seriate setae tend to be reduced in number and the general setae are relatively longer. There actually seems to be an inverse relationship between the length of the general setae relative to the diameter of the article on which they are borne and the degree of maturity of the specimen.

We thus have two sets of characters, the shape of the tergites and the length and arrangement of the setae on the legs, particularly those of the 15th metatarsus, which are dependant to a very great extent on degree of maturity. The validity of such species and subspecies as *P. baldensis* Verhoeff (1937), *P. fasciatus albanicus* Verhoeff (1934) and *P. fosciatus storkani* Verhoeff (1934), all depending on one or both of these characters for their definition, is therefore open to question.

Eupolybothrus (E.) litoralis (L. Koch)

The material which can undoubtedly be assigned to the typical form of *E. litoralis* is certainly conspecific with the specimens Verhoeff has labelled " Lithobius fasciatus graecus", but since the latter may represent a geographical race they should be regarded as belonging to a distinct subspecies unless it can be shown that their distinctive character is altogether unstable.

Eupolybothrus (E.) litoralis litoralis (L. Koch)

Figs. 8 to 12

Lithobius litoralis L. Koch, 1867, p. 899.
? *Lithiobius* (*Polybothrus*) *fasciatus graecus* var. *fasciatograecus* Verhoeff, 1901, p. 347.
not *Lithobius litoralis* Muralewitsch, 1906, p. 67.

MATERIAL EXAMINED. The following specimens, preserved in spirit, are present in the Koch Collection of Arachnida and Myriapoda in the British Museum (Natural History) ; except where otherwise stated, the labels appear to be in L. Koch's hand :

" L. litoralis " " Tinos Erber " (Reg. no. 13. 6.18. 368).

A single immature female 24 mm long. The locality label appears to be in L. Koch's hand but the identity label has been rewritten. As L. Koch's original description was based on a single immature female from Tinos (Aegean archipelago) I have no doubt that this specimen is the holotype and have labelled it accordingly.

" Lithobius grossipes C.K. " " Tinos Erber " (Reg. no. 13.6.18. 297).

A single male 38 mm long.

" Lithobius grossipes C.K. " " Rhodus Erber " (Reg. no. 13.6.18. 294–296).

A mature male 28 mm long, an immature male 18 mm long and an immature female 23 mm long.

DIAGNOSIS OF ADULT. Length up to 38 mm or more. Antennae up to 57 articles or more. Glandular pores of 15th leg concentrated on internal aspects of femur, tibia, tarsus and metatarsus only. 15th metatarsal general setae up to three-quarters the diameter of the article in length. 15th metatarsal seriate setae absent. Basal pit of male 15th femur extensive and deep. Internal dorsal sulcus of male 15th femur not extending to margin of pore-free area which is barely swollen. Coxolateral spines usually absent.

DESCRIPTION OF ADULT. Two males only. *Length* : 28 and 38 mm ; 15th legs two-thirds of body-length. *Colour* : uniform yellow. *Antennae* : two-thirds of body-length ; of 56 and 57 articles. *Ocelli* : 1+4, 5, 5, 3 with those of the superior row oval, and 1+4, 4, 4, 3 with those of the superior row almost round ; general pattern as described for *E. fasciatus*. *Prosternum* : with 8+8 small teeth ; lateral spines peg-like, placed immediately lateral to external teeth. *Tergites* : there is a greater tendency towards angulation and slight projection of the posterior angles of the large tergites, and towards sinuosity of the internal borders of the posterior projections on the short tergites (Fig. 10) than in most specimens of either *E. fasciatus* or *E. grossipes* but the difference in these respects is hardly consistent enough to be of diagnostic value ; posterior border of intermediate tergite sinuous. *Coxal pores* : 30 to 55 in four to five rows on each of the 12th to 15th coxae, most numerous on 14th. *Glandular pores of 15th legs* (Fig. 8) : concentrated on internal aspects only of femur, tibia, tarsus and metatarsus ; sparse on prefemur.

Chaetotaxy of 14th and 15th legs

General setae : on the metatarsus numerous, up to three-quarters the diameter of the article in length (Fig. 9) ; of much the same density and absolute length on the tarsus, about a quarter the diameter of the article in length ; on the tibia and femur (Fig 8) sparser and rather shorter ; on the dorsal aspect of the prefemur much the same as those on tibia and femur but on the ventral aspect of the article the setae are stout, almost spinous. *Seriate setae* : none on the 15th metatarsus ; as in *E. fasciatus* on the 14th leg. *Spinous setae* : on the 14th tarsus the ventral external seta (VaTa) is replaced by two small setae (Fig. 11), while the ventral internal seta (VpTa) is stout. *Setae of tuft* (Fig. 8) : long and numerous in both specimens.

Sculpturing of 15th legs (Fig. 8)

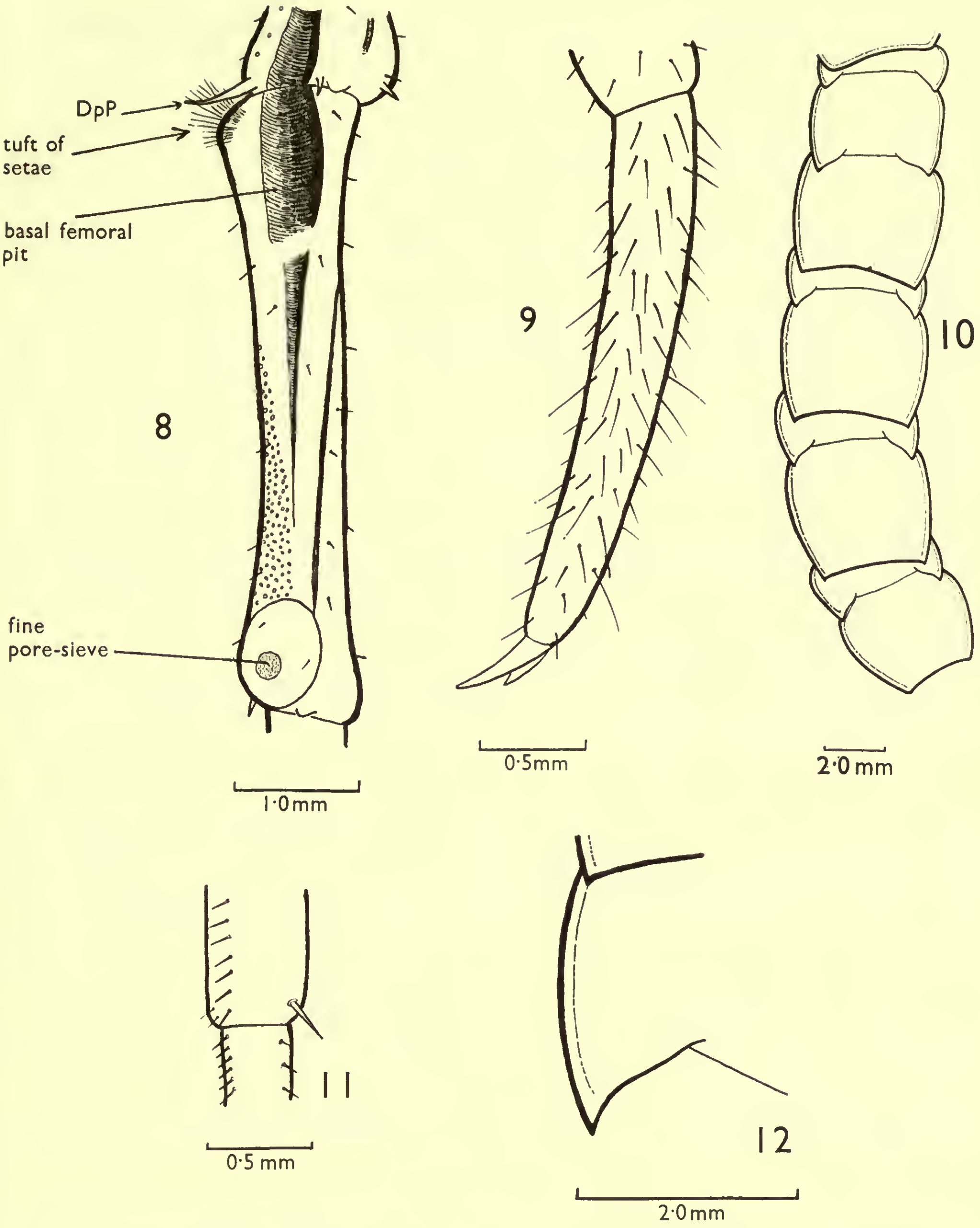
Prefemur with dorsal sulci distinct, internal one broad and deep, continuous with basal femoral pit, external one finer, not reaching the distal end of article ; basal femoral pit deep and extensive, scaphoid, occupying about half the diameter of the base of femur and a quarter of its length, not attenuated distally as in *E. fasciatus* but becoming shallower before leading to the internal femoral sulcus which then deepens and becomes gradually narrower and shallower distally to disappear before reaching the margin of the pore-free area ; external femoral sulcus finer, extending to the margin of the pore-free area ; pore-free area occupying about the distal one-fifth of the internal aspect of femur, slightly elevated without producing any marked swelling, bearing at its centre a well-circumscribed circular or slightly oval fine pore-sieve about a quarter the diameter of the distal end of femur ; setae on the pore-free area no denser than on the rest of the shaft and whether or not there are any actually on the pore-sieve seems quite fortuitous.

Sculpturing of 14th legs

Internal and external dorsal sulci rather indistinct on prefemur and femur.

Spinulation :

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	—	m	amp	amp	am	a	—	amp	a–p	a–p
15	—	m	amp	amp	am	a	—	amp	p	p


DpP
tuft of setae
basal femoral pit
fine pore-sieve
8
1·0 mm
9
0·5mm
10
2·0 mm
11
0·5 mm
12
2·0 mm

FIGS. 8 to 12. *Eupolybothrus litoralis litoralis*. 8. Femur and distal part of prefemur of 15th leg (dorsal view). 9. Metatarsus of 15th leg (external view). 10. 6th to 14th tergites (dorsal view). 11. Region of tarso-metatarsal articulation of 14th leg to show seriate and spinous setae (ventral view). 12. Posterior projection of 13th tergite (dorsal view). Figs. 8 to 11 taken from a ♂ from Tinos (38 mm long); fig. 12 taken from an immature ♀ from Rhodes (23 mm long).

15 VpF and 15 DpT may be absent ; a small coxolateral spine on right 15th leg of the male from Rhodes only ; a well-developed 15th accessory apical claw.

Genitalia : as in *E. fasciatus*.

Immature specimens. *The male from Rhodes* (lacking the 14th and 15th legs), 18 mm long with 41 antennal articles, 1+3, 4, 3 ocelli, 7+7 prosternal teeth, setiform lateral spines, about 15 pores on each of the posterior coxae and no coxolateral spines seems, judging by the development of the genitalia, to belong to the fourth post-larval stadium.

The female holotype from Tinos, 24 mm long, with 44 antennal articles, 1+4, 4, 3 ocelli, 7+7 prosternal teeth, setiform lateral spines, about 18 pores on each of the posterior coxae, no coxolateral spines and adult spinulation on the 14th and 15th legs, has the 15th metatarsal general setae rather longer than the diameter of the article and the tarsal setae about half the diameter of the article in length. In spite of its size this specimen seems also to belong to the fourth post-larval stadium because each gonopod bears only a single minute spur and a small claw.

The female from Rhodes, 23 mm long, resembles the above specimen but for a pair of incipient teeth adjacent to the median prosternal notch (making a total of 8+8), 30 to 35 pores on each of the posterior coxae and more advanced genitalia with two small unequal spurs and a well-developed claw on each gonopod. It certainly belongs to the fifth post-larval stadium.

The tergites of all these specimens tend to show features of immaturity comparable to those found in *E. grossipes* and the posterior projection of the 13th tergite of the last specimen is figured (Fig. 12).

Discussion. Latzel (1880) regarded *Lithobius litoralis* as a synonym of *L. grossipes* (= " *L. fasciatus* " of more recent authors) and this synonymy has not hitherto been disputed. This is hardly surprising because L. Koch's description of the single immature female might well apply to *E. grossipes*. But examination of the holotype shows it to be distinct from this species owing to the distribution of concentrated glandular pores on the 15th legs, and also from *E. fasciatus* owing to the absence of 15th metatarsal seriate setae. Further, the adult male from Tinos (the type locality), although labelled " L. grossipes " by Koch, is clearly of the same species as the holotype and the sculpturing of its 15th femur is characteristic. Koch defines *litoralis* by means of immature characters only, notably the rather undeveloped gonopods, and was unaware of its true nature ; otherwise he would not have identified other specimens of *litoralis* in his collection as *L. grossipes*. He may thus be said to have named *E. litoralis* accidentally.

Lithobius fasciatus graecus Verhoeff, which is described below, is considered here to be conspecific, though not consubspecific, with *E. litoralis*, differing only in the constant possession of coxolateral spines. *L. fasciatus graecus* var. *fasciatograecus* Verhoeff, which was originally described from Naxos and Crete (Verhoeff, 1901) as a variety without coxolateral spines, is therefore almost certainly identical with the nominate subspecies of *E. litoralis*.

Eupolybothrus (E.) litoralis graecus (Verhoeff), n. comb.

Lithobius (Polybothrus) fasciatus graecus Verhoeff, 1899, p. 434, fig. 1a.

Material examined. The following specimens, preserved in spirit, are present in the Verhoeff Collection of Myriapoda in the British Museum (Natural History) and are labelled " Lithobius fasciatus graecus Verhoeff. " " Greece " (Reg. no. 03.8.25. 47–49) :

An immature male 23 mm long in a fair state of preservation, a mutilated mature female about 26 mm long in two separate fragments lacking most of the appendages, and a mutilated immature female 22 mm long lacking most of the legs. Verhoeff's (1899) original description of *L. fasciatus graecus* was based on a number of examples from several localities in southern Greece and it is probable that these specimens are part of the syntypical series.

Diagnosis of adult. As nominate subspecies except for the presence of one or two well-developed coxolateral spines on each of the 15th and sometimes also on each of the 14th or 12th to 14th legs.

Description of adult. A mutilated and fragmented female only ; detached telopodites of 14th and 15th legs seem to belong to this specimen and their characters are included in the following description.

Length : 26 mm ; 15th leg 15 mm. *Colour* : uniform yellow. *Antennae* : broken. *Ocelli* : 1+4, 4, 4, 2. *Prosternum* : with 8+8 small teeth, the internal pair being only incipient ; lateral spines peg-like, lateral to external teeth. *Tergites* : as figures for *E. l. litoralis* (Fig. 11). *Coxal pores* : 20 to 30 very unequal in size in four rows on each of the 12th to 15th coxae. *Glandular pores of 15th legs* : as in *E. l. litoralis.*

Chaetotaxy of 14th and 15th legs

General setae : as in *E. l. litoralis*. *Seriate setae* : none of the 15th metatarsus ; on the 14th metatarsus the external row well-defined but the internal row absent ; on the 14th tarsus rather sparse. *Spinous setae* : as in *E. l. litoralis.*

Spinulation :

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	a	m	amp	amp	am	a	—	amp	a–p	a–p
15	a	m	amp	amp	a	a	—	amp	p	p

Coxolateral spines (VaC) present on each of the 12th to 15th legs; a well-developed 15th accessory apical claw.

Genitalia : as in *E. fasciatus*

Immature stadia

Male fifth post-larval stadium (*pseudomaturus*)

Differs from the adult in the following characters. *Length* : 23 mm. *Antennae* : three-fifths of body-length ; of 45 articles. *Ocelli* : 1+4, 4, 2, 2. *Prosternum* :

with 7+7 teeth ; lateral spines setiform, lateral to external teeth. *Coxal pores* : 13 to 18. *General setae of 14th and 15th legs* : on the metatarsus about as long as the diameter of the article, on the tarsus about half the diameter of the article in length. *Seriate setae of the 14th leg* : on the metatarsus the internal row present but reduced to a few small setae ; on the tarsus very sparse. *Setae of tuft* : absent. *Scuplturing of 15th leg* (left only) : dorsal sulci of prefemur indistinct ; basal femoral pit and internal femoral sulcus quite distinct but less well defined than in adults of *E. l. litoralis* ; external femoral sulcus indistinct ; pore-free area occupying about the distal one-fifth of the internal aspect of femur with neither swelling nor fine pore-sieve. *Sculpturing of 14th legs* : dorsal sulci on prefemur and femur very faint. *Spinulation* : 15 VmT present ; 14 DaC absent ; two coxolateral spines on left 15th leg, one on right 15th leg, none on 12th to 14th legs. *Genitalia* : posterior border of genital sternite with a feeble median notch and about 8 marginal setae on either side ; gonopods very slender, basal article about half the length of distal article.

Female fifth post larval stadium (*pseudomaturus*)

Differs from the male in the following characters : *Length* : 22 mm. *Antennae* : 42 articles. *Ocelli* : 1+4, 3, 3, 1. *Coxal pores* : 13 to 16. *Coxolateral spines* : one on each of 14th and 15th legs. *Genitalia* : two small unequal spurs and a well-developed claw on each gonopod.

DISCUSSION. In his original description of *Lithobius fasciatus graecus*, Verhoeff (1899) mentions the relatively pale colour, the marked posterior emargination of the large tergites and the presence of one or two coxolateral spines on each 15th leg. The projecting posterior angles of the large tergites in Koch's specimens of *E. litoralis* (Fig. 10) accentuate the general appearance of emargination and this character together with the pale colour and also the presence of a coxolateral spine on one 15th leg of a male from Rhodes leads to the suspicion that *graecus* may be identical with *litoralis*. However, Verhoeff (1899) describes the male 15th femur as resembling that of " *fasciatus* " and makes no mention of the chaetotaxy or pore-distribution on the 15th legs ; later the same author (Verhoeff, 1941 : 105), when discussing these characters, states that he had no material referable to *graecus* available for examination. We would therefore be uncertain as to the identity of *graecus* were it not for the specimens purchased from Verhoeff by the British Museum which show the same pore-distribution and almost the same chaetotaxy as *E. litoralis* ; the 15th femur of the single immature male shows just the sort of sculpturing to be expected in a comparable stadium of *E. litoralis* so there is little doubt that Verhoeff's specimens of *graecus* and Koch's specimens of *litoralis* are conspecific. The slight deficiency in the seriate setae and the number of coxal pores of the former as compared with the latter is probably fortuitous but the presence of well-developed coxolateral spines in both mature and immature examples of *graecus* contrasts with their absence from all but one example of *litoralis*, and this specimen shows a small spine on the right side only.

In the present state of our knowledge of the distribution of these forms it cannot be more than a matter of opinion as to whether we regard the coxolateral spines as altogether unstable and *graecus* as identical with *litoralis*, or whether these spines should be regarded as characteristic of a subspecies from the mainland of Greece, occurring only occasionally in the nominate subspecies from the islands. The latter view has been adopted here although further collecting may well prove it to be incorrect.

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